Fish Utilisation of Saltmarshes and Managed Realignment areas in SE England

by

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This thesis is dedicated to *Team fish*:

Dad, Mum, Shaba, Cloughy, Kirk & Drew

Abstract

Saltmarshes in SE England are eroding rapidly and one potential impact is the loss of habitat for fishes. Saltmarshes have been created by setting back the existing line of flood defence through managed realignment. The use by fishes of natural and managed realignment habitats at Tollesbury, Abbotts Hall and Orplands was examined (2005-07).

Three seasonal groups were apparent in the fish assemblages of the managed realignment sites: February-April (*Pomatoschistus microps* and *Sprattus sprattus*), May-September (*Dicentrarchus labrax* and *Atherina presbyter*) and October-January (*Liza aurata* and *Liza ramada*). The sites were used mainly by 0- and 1-group fishes and adult *P. microps*. The mean abundance (July - August 2007) was 558 0.1 ha^{-1} (range 76 - 2699 0.1 ha^{-1}).

In summer, small (<30 mm) zooplanktivorous *D. labrax* fed successfully at all sites. Larger (30-59 mm) *D. labrax* consumed more macroinvertebrates in the Tollesbury managed realignment and two established marshes than at Abbotts Hall and Orplands. By autumn there were no site-specific differences in gut fullness of *D. labrax*. Stable isotope ratio analysis and gut contents analysis revealed that small (<50 mm) *D. labrax*, *S. sprattus* and *A. presbyter* assimilated zooplankton which eat detritus, resuspended microphytobenthos and some phytoplankton. *L. aurata* assimilated zooplankton and microphytobenthos. *P. microps* (20-50 mm) and *A. presbyter* (80-99 mm) assimilated benthic meiofauna. Larger (50-230 mm) *D. labrax* assimilated macroinvertebrates which eat microphytobenthos, *Ulva* spp., C_3 plants and detritus.

Some recommendations for saltmarsh restoration are provided with an estimate of the economic value of bass in saltmarshes, to highlight further areas of research.

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I certify that this thesis, and the research to which it refers, are the product of my own work and that any ideas or quotations from the work of other people, published or otherwise are fully acknowledged in accordance with standard scientific referencing practices.

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Chapter 1: General Introduction

Definition of saltmarshes

Coastal saltmarshes are areas of vegetation where particulate intertidal sediments in wave-sheltered temperate environments, often estuaries, are colonised by herbaceous halophytic plants (Adam 1990; Elliott and Hemmingway 2002). They are inundated fully only on high spring tides and the vegetation usually extends down to mean high water neap tide level. In many parts of the UK including SE England the transition from saltmarsh to terrestrial vegetation grassland is truncated by sea walls. Saltmarshes are normally fronted by mudflats and are often dissected by complex creek systems, which channel floodwater into and out of the saltmarsh on the flood and ebb tides (Adam 1990; Little 2000; Pye 2000; Fagerazzi and Furbish 2001; Elliott and Hemmingway 2002).

Saltmarsh characteristics

Coastal saltmarshes are presumed to develop by facilitated succession where sediments that accumulate in wave-sheltered environments are colonised by plants that promote further sediment accretion, by slowing water movement and by stabilising the sediment with their roots. Saltmarsh development is a highly complex process and is affected by a number of factors. These variables include site-specific tidal characteristics, wave action and hydrology (e.g. Mitsch and Gosselink 1993); the rate of sediment accretion, the elevation and the surface drainage (Long and Mason 1983; Mitsch and Gosselink 1993; Hughes 2001; Crooks et al. 2002; Lindig-Cisneros and Zedler 2002; Spencer et al. 2008); freshwater inputs, the salinity and the chemistry of the soil and surface waters (Adam 1990; Vernberg 1993; N.R.A. 1995; Crooks and Pye 2000; Feist and Simenstad 2000; Noe and Zedler 2001; Mason et al. 2003; Zedler et al. 2003); as well as the shoreline structure and site topography (N.R.A. 1995; Desmond et al. 2000; Eertman et al. 2002). Saltmarsh plant species show a vertical zonation where the lower limit of each species is determined by their tolerance to factors associated with inundation by sea water and the upper limit by biological interactions, particularly interspecific competition with plant species less able to tolerate inundation (Adam 1990).

Whereas North American saltmarshes are dominated by *Spartina* spp., western European saltmarshes contain a range of plant species including cord grass *Spartina* spp., glasswort *Salicornia europaea*, sea blight *Suaeda maritima*, common saltmarsh grass *Puccinellia maritima*, sea lavender *Limonium vulgaris*, sea aster *Aster tripolium* and sea purslane *Atriplex portulacoides* (Jackson et al. 1985; Burd 1992; Bakker et al. 1993). In the UK, the dominant species are *P. maritima* and *A. portulacoides* and the saltmarshes develop as plateaux at the elevations where these species grow best and forming dense vegetation cover.

Other photosynthetic organisms that are present in saltmarshes include the green algae *Ulva* spp., the microphytobenthos including epipelic diatoms, and in less turbid habitats, phytoplankton (Elliott and Hemmingway 2002; Galvan et al. 2008). The autochthonous detritus produced by all of the photosynthetic organisms described above, as well as the allochthonous detritus originating from adjacent terrestrial, marine and freshwater habitats and from sewage, are potential basal resources for a wide range of coastal and marine food chains (Fry 2006).

The value of saltmarshes

As saltmarshes buffer the transition between the land, freshwater and the sea (Boorman 2000), they sustain important biological, chemical and hydrological functions (Lefeuvre et al. 2000). One such function is the production and transfer of organic matter. Unlike North American saltmarshes, European saltmarshes tend to be net importers of organic material because they are only inundated by spring tides; for example, less than 1% of the organic matter produced is exported as macro-detritus (Dankers et al. 1984; Hemminga et al. 1992; Hemminga et al. 1993; Boorman 2000; Bouchard and Lefeuvre 2000). Fishes may also be important vectors of organic material from saltmarshes to estuaries (Kneib and Wagner 1994; Laffaille et al. 1998; Lefeuvre et al. 1999; Maes and Ollevier 2000; Laffaille et al. 2002; Stevens et al. 2006).

In addition to these ecological functions, saltmarshes also protect the sea walls that offer flood protection to low-lying coastal hinterlands by attenuating wave and tidal energy (King and Lester 1995; Dixon et al. 1998; Möller 2003). They may maintain water quality by filtering the water before it ebbs to the sea, and have important nitrogen, carbon and pollution storage functions (Jickells et al. 2003). They are also socio-economically valuable as sites of agriculture (grazing), education, tourism, leisure, and recreation (Spurgeon 1999).

The value of saltmarsh habitats is now recognised internationally and nationally. For example the UK government has declared a 'Biodiversity Habitat Action Plan' for saltmarsh under the Convention on Biological Diversity (United Kingdom Biodiversity Group 1999), and is committed to restoring and maintaining the total saltmarsh area to that present in 1992 which has equated to 60 ha yr^{-1} since 1992 (Paramor and Hughes 2005). To comply with the EU Water Framework Directive (2000/60/EC) all EU member states are required to conduct statutory monitoring of brackish habitats, within transitional water bodies. The development of a biological monitoring procedure is required to ensure that saltmarshes are protected and restored, to achieve 'Good

Ecological Status' or 'Good Ecological Potential', by 2015 (Pollard and Huxham 1998; Elliott et al. 1999). One aspect of this process may involve the determination of the ecosystem functioning of saltmarshes, for example as fish nursery habitats (Best et al. 2007).

Saltmarsh fauna

Saltmarshes provide refugia, feeding and breeding grounds for meiofauna (Fleeger et al. 1984; Gregg and Fleeger 1997), macroinvertebrates (Mason et al. 1991), birds (Rupp and Nicholls 2002) and fishes (Laffaille et al. 2000a; Stevenson 2002; Hampel et al. 2003; Colclough et al. 2005). The resident saltmarsh invertebrate fauna is generally dominated by a low number of species with a high abundance (Drake and Arias 1991a; Laffaille et al. 2000). As transitional habitats, saltmarshes are also inhabited by a number of terrestrial species which are either residents or use the marsh for different periods of the year.

The invertebrates that commonly inhabit European saltmarshes include polychaetes such as *Nereis (=Hediste) diversicolor* (Jackson et al. 1985; Frid and James 1989; Creach et al. 1997; Paramor and Hughes 2004), oligochaetes such as *Tubifex* spp. (Mason et al. 1991; Hampel et al. 2005), mysid shrimps *Neomysis integer* (Mees and Hamerlynck 1992; Maes et al. 2003), prawns such as *Palaemon* spp. (Frid and James 1989; Cabral and Costa 2001; Koutsogiannopoulou and Wilson 2007), brown shrimp *Crangon crangon* (Cattrijsse et al. 1994; Sa et al. 2006; Koutsogiannopoulou and Wilson 2007), amphipods such as *Corophium volutator* (Jackson et al. 1985; Mason et al. 1991; Gerdol 1994; Creach et al. 1997; Hughes and Gerdol 1997) and *Orchestia* spp. (Laffaille 2001; Dias and Hassall 2005), shore crabs *Carcinus maenas* (Frid and James 1989; Mason et al. 1991; Cattrijsse et al. 1994), nematodes (Bolam et al. 2006), ostracods (Horne and Boomer 2000), isopods (Mason et al. 1991; Thorin et al. 2001; Dias and Hassall 2005; Garbutt et al. 2006), gastropods such as *Hydrobia ulvae* (Kay and Knights 1975; Jackson et al. 1985; Beardall et al. 1990; Fish et al. 2000; Atkinson et al. 2004) and bivalves such as *Macoma balthica* (Hampel et al. 2005). Invertebrates of terrestrial origin found in saltmarshes include spiders and insects particularly Diptera larvae, planthoppers, springtails and bristletails (Mason et al. 1991).

North western European tidal saltmarshes are often characterised by a high abundance of fishes which breed and reside in the estuary, particularly species belonging to the Gobiidae, as well as juveniles of other marine species (Mathieson et al. 2000; Hampel and Cattrijsse 2004). Some fishes that occur commonly in European saltmarshes include, gobies such as the common goby *Pomatoschistus microps*, transparent goby *Aphia minuta*, and sand goby *Pomatoschistus minutus*; the eel *Anguilla anguilla*; clupeids such as herring *Clupea harengus*, sprat *Sprattus sprattus*, and anchovy *Engraulis encrasicolus*; pipefish such as Nilsson's pipefish *Syngnathus rostellatus* and the greater pipefish *Syngnathus acus*; sea bream *Sparus aurata*, and *Diplodus* spp.; thin lipped grey mullet *Liza ramada*; bass *Dicentrarchus labrax*; and flatfishes such as flounder *Platichthys flesus*, plaice *Pleuronectes platessa*, sole *Solea solea* and *Solea senegalensis* (Drake and Arias 1991a; Colclough et al. 2000; Lefeuvre et al. 2000; Baldo and Drake 2002; Mees et al. 2005; Cattrijsse and Hampel 2006; Viega et al. 2006; Koutsogiannopoulou and Wilson 2007).

The benefits of saltmarshes for fishes

The value of natural and restored saltmarshes as fish nursery areas has been studied extensively in the USA (Shenker and Dean 1979; Weinstein 1979; Bozeman and Dean 1980; Boesch and Turner 1984; Rozas and LaSalle 1990; Kneib 1997; Desmond et al.

2000; West and Zedler 2000; Madon et al. 2001; Minello et al. 2003), and more recently, in Europe (Lancaster 1991; Drake and Arias 1991a; Laffaille et al. 1998; Mathieson et al. 2000; Cabral and Costa 2001; Cattrijsse and Hampel 2006). The conservation of intertidal habitats is now an important component of integrated fisheries management (Crooks and Turner 1999).

The nursery function of saltmarsh habitats for fish has been attributed to refuge from predation (Shenker and Dean 1979; Boesch and Turner 1984; Paterson and Whitfield 2000; Hampel et al. 2005). Fewer predators are present in the shallowest intertidal habitats than subtidally (Mathieson et al. 2000). However, confluences and creek mouths have been shown to be preferred habitats for small predatory piscivorous fishes, which are limited more by the absence of fish prey than by the low water clarity (Kneib 1997; Simenstad et al. 1998; Reid et al. 1999; Tupper and Able 2000; Sheaves 2001; Colclough et al. 2005). The high turbidity of saltmarsh habitats offers increased protection from visual predators (Blaber and Blaber 1980; Cyrus and Blaber 1987; Cattrijsse et al. 1994) and changes in turbidity may affect interactions between predators and their prey in different ways (Skov et al. 2007).

Small fishes can feed in relative safety in saltmarsh habitats (Rozas et al. 1988; Rozas and LaSalle 1990; Archambault and Feller 1991; Kneib 1997; Cabral and Costa 2001; Laffaille et al. 2001c; Madon et al. 2001; Nemerson and Able 2003; Hampel et al. 2005). The main value of these habitats as feeding areas is reflected in the increased gut fullness of fishes leaving these sites compared with when they entered them (Rozas and LaSalle 1990; Cattrijsse et al. 1994; Kneib and Wagner 1994; Elliott and Hemmingway 2002) and in the diets of fishes which often contain a large proportion of saltmarsh resident species (Rountree and Able 1992; Laffaille et al. 2001c; Nemerson and Able

2003; Hollingsworth and Connolly 2006). In addition to tidal variations in feeding, some fishes are affected by prey activity and exhibit diurnal and lunar rhythms in their use of the saltmarshes (Robin and Marchand 1986; Archambault and Feller 1991; McMahon and Holanov 1995; Methven et al. 2001; Hibino et al. 2006). For example the goby *P. minutus* is a more active feeder during the day on spring tides and during the night on neap tides, however the reason for this difference is not known (Hampel and Cattrijsse 2004). Other spatio-temporal influences on the use by fishes of these transitional habitats include variations in salinity (Peterson and Ross 1991; Gillanders and Kingsford 2002; Rubio et al. 2005), dissolved oxygen (Wannamaker and Rice 2000; Smith and Able 2003), and temperature (Russel et al. 1996; Koumoundouros et al. 2002).

The majority of studies of fish use of saltmarshes in Europe are based in the mouths of creeks because fishes can only access the vegetated saltmarsh plateaux when it is flooded by tides higher than high neap tides. Large quantities of detritus at the head of the creeks in the high intertidal areas may attract detritivorous invertebrates, which may in turn attract secondary consumers (Rozas and Odum 1987). A number of invertebrates including talitrid amphipods, beetles and flies seek refuge within and feed upon, the marsh vegetation and the detritus of the strandline (Mason et al. 1991). These organisms may form important feeding links to secondary consumers when the marsh is flooded (Weisberg et al. 1981; Boesch and Turner 1984; Laffaille et al. 1999; Laffaille et al. 2000b; Laffaille 2001; Laffaille et al. 2005). Savino and Stein (1989) suggested that predators only seek vegetated habitats if appropriate prey are present. Large numbers of fishes have also been reported to use semi-permanent water bodies or ponds in restored saltmarshes (Colclough et al. 2005). The depth of the pond at low tide, the presence of submerged aquatic vegetation within the pond (Rozas and Odum 1987; 1988), the degree of tidal flushing and the food availability, are all important factors which will determine the survival and growth rates of fishes using these ponded areas. In general habitats which are more heterogeneous are perceived to be more beneficial to fishes, as the habitat structural complexity is important in shaping fish assemblages (Duffy-Anderson et al. 2003).

The biology of bass, *Dicentrarchus labrax* (L.)

A species of particular interest in this study is the European sea bass, *Dicentrarchus labrax* (Family Serranidae, Order Perciformes). This species has a geographical range extending from Southern Norway to North Africa, the Mediterranean and adjoining seas (Wheeler 1978). The slow growth, late maturity and long lifespan of *D. labrax* in Britain is indicative of this species being close to the northern limits of its range (Claridge and Potter 1983; Lancaster 1991) and these attributes make it particularly susceptible to over-exploitation (Kelley 1988a). Despite this, *D. labrax* has become one of the most abundant and commercially exploited species in Europe since the 1970s (Wheeler 1978; Pickett and Pawson 1994). The timing of bass spawning is dependent on the temperature (11-15°C) and latitude (Barnabe 1990; Jennings 1990) and involves the release of ripe ova in two to three batches over a two to three week period (Mayer et al. 1990). Spawning in the UK occurs from February to May in offshore waters and from May to June in shallow inshore waters, with the youngest and first-time spawners more likely to spawn inshore (Dando and Demir 1985; Sabriye et al. 1988a; Jennings 1990; Colclough et al. 2004).

The juveniles of *D. labrax* migrate inshore becoming abundant in saltmarshes from May which they frequent throughout the summer months before migrating to deeper waters in the autumn (Kelley 1986; 1988a; Lancaster 1991; Pickett et al. 1994). In the UK all non-polluted estuaries from the Ribble Estuary in NW England to the Blackwater Estuary in SE England are likely to be nursery habitats for this species (Kelley 1988a). The fish in their second year of life ('1-group') return to these intertidal habitats in the following summer. The 0- and 1-group movements occur in shoals of 7-15 individuals but can involve up to 30 fish (personal observations) and bass up to 1 kg display shoaling behaviour (Colclough et al. 2004). The autumnal migrations are extended every year into progressively deeper waters until recruitment to the adult stock at the age of 5 or 6 years (Lancaster 1991; Kelley 2002; Colclough et al. 2004). The adults migrate seasonally between inshore feeding grounds to offshore wintering and pre-spawning habitats.

There is considerable interest in *D. labrax* because of its economic importance to both the UK recreational and commercial fishing industries. Since 1990, the legal minimum landing length has been 36 cm in most areas of the UK, which is less than the average length of a fecund female, leaving the species open to over-exploitation. The extent to which this species depends upon estuaries and saltmarsh habitats is not known, but the high abundance of small *D. labrax* in such habitats has been highlighted previously as an important indicator of the nursery value of these areas (Claridge and Potter 1983; Kelley 1986; Lancaster 1991). The first year of life of *D. labrax* is critical in determining the strength of that year class in future years (Kelley 1988a; Lancaster 1991); therefore the habitats that sustain 0-group *D. labrax* during this period are valuable and must be conserved (Jennings 1992). In addition to the pressures from inshore pollution and climate change, the extent to which undersized bass are illegally fished from estuaries and inshore areas is unknown, but thought to be considerable (S. Colclough personal communication).

Although previous writers have considered the diets of juvenile *D. labrax* in captivity (Kennedy and Fitzmaurice 1972; Sabriye et al. 1988a) and in natural habitats (Claridge and Potter 1983; Aprahamian and Barr 1985; Dando and Demir 1985; Kelley 1986; Sabriye et al. 1988a), none has investigated the feeding benefits to *D. labrax* in saltmarshes in SE England.

Saltmarsh loss in SE England

Almost all saltmarsh areas in SE England have experienced net erosion in the past 50 years (Burd 1992; Pye 2000). This loss is estimated at 2 % yr^{-1} (Dixon et al. 1998) with deleterious consequences for conservation and flood defence interests (Hughes and Paramor 2004; Paramor and Hughes 2004). The causes of this loss include an ever-expanding pressure for land claim to develop ports, harbours, industry, housing, and agriculture (McClusky and Bryant 1992). In SE England the loss of saltmarsh is particularly severe and the explanation accepted by the responsible government agencies (Environment Agency and Natural England) is coastal squeeze, where the isostatic sinking of the land leads to local sea level rise. Under conditions of sea level rise saltmarshes migrate inland but this is prevented by the sea walls that protect the low-lying hinterland. Hughes and Paramor (2004) suggested that coastal squeeze may not be responsible for loss of saltmarsh, rather bioturbation and herbivory by the ragworm *Nereis diversicolor* and the amphipod *Corophium volutator* may be responsible for much of the loss of saltmarsh (Gerdol and Hughes 1993; Paramor and Hughes 2004; 2005; 2007). Mason et al (2003) also suggested that increasing use of herbicides may reduce the cohesive strength of the sediment, by removing the epipelic diatoms, leading to increased erosion. One element of saltmarsh loss in SE England not fully considered hitherto is the impact of this loss on the juvenile fishes that use saltmarshes during a vital period of their development.

Managed realignment of the coast

The main policy for creating new areas of saltmarsh in the UK, and particularly in SE England, is 'managed realignment' of the coast. This process involves the breaching of existing flood defences, to allow the conversion of old agricultural land behind the sea wall, into intertidal habitats. Although invertebrates and fishes may colonise the new habitats soon after restoration (Tupper and Able 2000) the replacement of the structural complexity of wetlands may take longer and be difficult to predict and achieve (Zedler and Callaway 1999; Zedler 2000; Zedler and Callaway 2000; Strange et al. 2002; Craft and Sacco 2003). However, some studies have highlighted successful examples of the restoration of certain forms of coastal habitat (Craft et al. 1999; Ledoux et al. 2003; Miller and Able 2002; Roman et al. 2002; Able et al. 2003; Jivoff and Able 2003; Teo and Able 2003; Able et al. 2004; Nemerson and Able 2005). Elements that are considered important in the restoration of saltmarshes include the development of a creek system, the presence of semi-permanent water bodies and marsh edge habitats (Minello and Zimmerman 1992; Zedler and Callaway 1999; Colclough et al. 2004; Colclough et al. 2005).

The first managed realignment sites in SE England, such as Tollesbury and Orplands, were developed for flood defence purposes (Pethick 2002). Newer sites such as Wallasea Island managed realignment site, were developed as habitat compensation for land claimed through port developments. At some sites, such as Horsey Island managed realignment site in Hamford Water, reused dredged harbour sediments were used to increase the elevation of the sites to facilitate vegetation establishment in areas where the salt marsh was eroding. At Abbotts Hall managed realignment site, an education centre was developed, and small-scale commercial harvesting of sea lavender honey and samphire was trialled.

Now, there is growing interest in quantifying and maximising the total economic value of each site through multiple benefits, such as the biogeochemical, socio-economic, and ecological functioning of the sites, including their use by fishes. It is within this context that the fisheries component of the 'Combined Functions in Coastal Zone Management' project was developed.

General aims

The aims of this study were to determine aspects of the fish use of saltmarshes and some managed realignment sites in SE England. The objectives were:

a) to develop a method for the qualitative and quantitative sampling of fishes in ancient and restored saltmarshes in macrotidal estuaries

b) to identify the seasonal variations in the fish assemblages using these habitats

c) to assess the value of different habitats to bass *Dicentrarchus labrax* a common and economically important species, by assessing the spatial and temporal variations in their diet, in managed realignment sites and adjacent ancient saltmarshes

d) to determine the ultimate sources of primary productivity for fishes and to identify the trophic interactions of juvenile fishes and their prey in three different managed realignment sites and

e) to offer recommendations for further research and in the design of future managed realignment schemes

The Blackwater Estuary was chosen as the focus of this research because there are three managed realignment sites (Tollesbury, Abbotts Hall and Orplands) in close proximity on this estuary, which are different in terms of their microhabitats and topography. See Chapter 2 for further details of the sites.

Outline of the thesis

In Chapter Two, a description of the field sites including some environmental parameters are provided. The development of the methods used to catch the fishes are described and discussed in relation to the strengths and weaknesses of various fish capture techniques. In Chapter Three, data on the seasonal variations in the fish assemblage are presented and discussed, with emphasis on bass *Dicentrarchus labrax*. Chapter Four describes the diets of 0- and 1-group *D. labrax* including temporal (seasonal and tidal) and spatial (managed realignment sites and adjacent established saltmarshes) variations. In Chapter Five, stable isotope analysis was used to investigate the positions of the fishes and their invertebrate prey in the food webs in three managed realignment areas in summer 2007. The sources of primary productivity at the base of the food webs are determined and the trophic level of these fauna are described. In Chapter Six, a summary of the main results is presented and the results are discussed in relation to the value of different managed realignment sites for fishes, in particular bass *D. labrax* and areas for future research.

Chapter Two: Methods

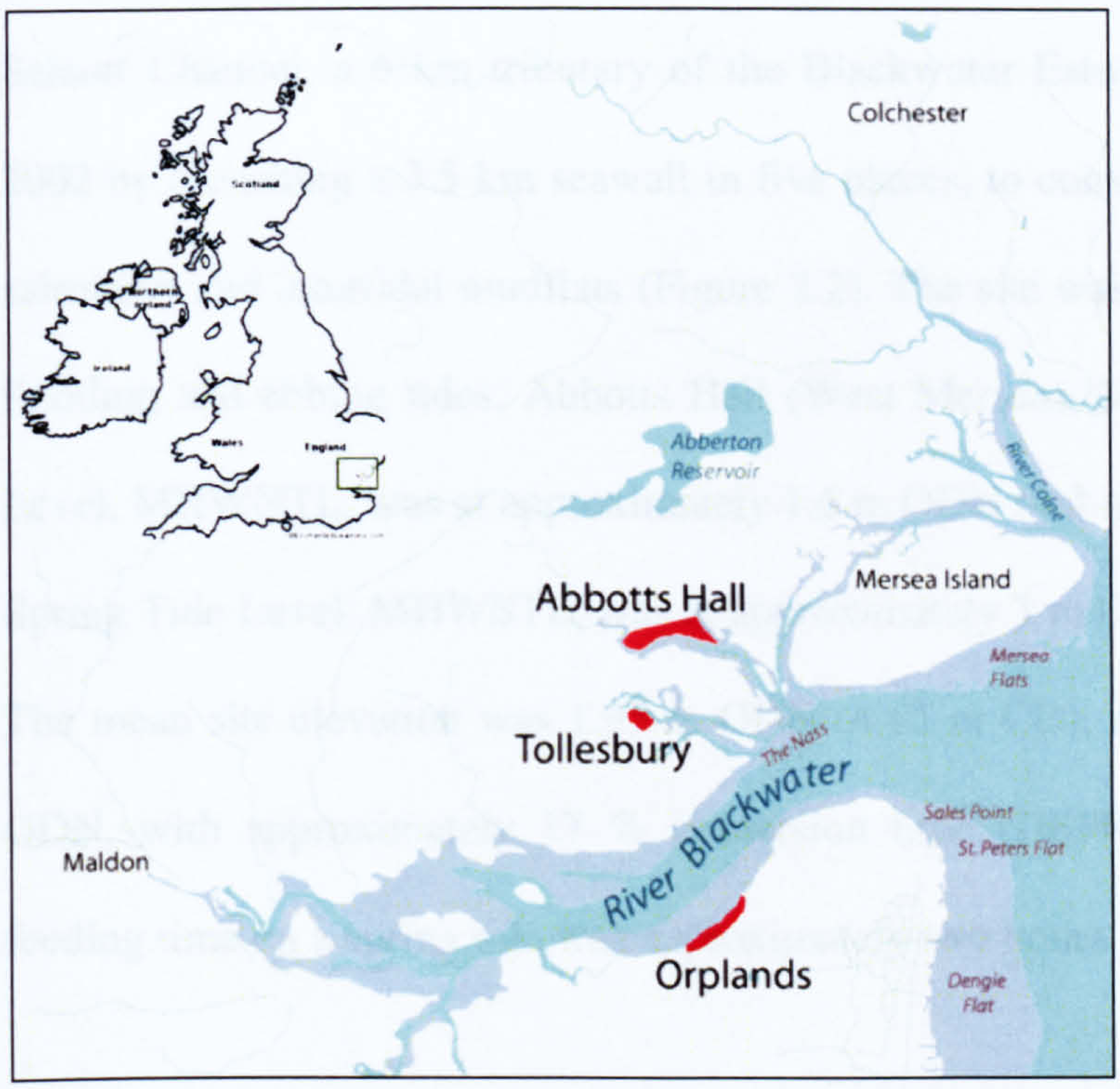
Field sites

The Blackwater Estuary in Essex, S.E.England, is a tributary of the Greater Thames Estuary, draining into the Southern North Sea. The Blackwater is the largest estuary in Essex (23 km long) with a catchment area of 1200 km^2. The majority of the Blackwater is less than 10m chartered depth and is bounded by extensive mudflats (Fox et al. 1999). This estuary also contains the largest area of saltmarsh in Essex (over 1000 hectares) (Chesman et al. 2006). The estuary receives relatively low freshwater riverine discharges in relation to the tidal prism and is well mixed, with a semidiurnal macrotidal regime (Talbot 1967; Chesman et al. 2006).

The study was based at three restoration sites in the Blackwater Estuary: Abbotts Hall, Tollesbury and Orplands managed realignment sites (Figure 2.1). Monthly fish samples were collected during daylight, flooding and ebbing spring tides between August 2004 and January 2007, at Abbotts Hall, Tollesbury and Orplands realignment sites and in the adjacent marshes at Tollesbury and Abbotts Hall. There were no natural marshes adjacent to Orplands managed realignment.

All elevations are given in metres above Ordnance Datum (ODN) and metres above Chart Datum (CD). The elevations were converted from ODN to CD using Admiralty Tide Tables (2001). Conversion factors were 2.68 m at Orplands (Bradwell waterside); 2.70 m at Abbotts Hall (Blott and Pye 2004); and 2.16 m at Tollesbury (Watts et al. 2003; Paramor and Hughes 2005).

Figure 2.1: The locations, in South East England, of Abbotts Hall, Tollesbury and Orplands managed realignment sites (in red) in the Blackwater Estuary



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Abbotts Hall

The Abbotts Hall managed realignment is located north of Abbotts Hall Saltings on the Salcott Channel, a 6 km tributary of the Blackwater Estuary. The site was created in 2002 by breaching a 3.5 km seawall in five places, to convert 40 ha of arable land into saltmarsh and intertidal mudflats (Figure 2.2). The site was sampled at breach C on the flooding and ebbing tides. Abbotts Hall (West Mersea), Mean High Water Neap Tide Level, MHWNTL, was at approximately 1.6 m ODN (4.3 m CD) and Mean High Water Spring Tide Level, MHWSTL, was at approximately 3 m ODN (4.7 m CD) (Jain 2004). The mean site elevation was 1.95 m ODN (4.65 m CD), ranging from 0.1 m to 4.1 m ODN, with approximately 17 % immersion time (DEFRA 2004). The average fish feeding time on a spring tide was approximately two hours.

The area sampled inside breach C contained two different habitats, and was divided approximately in half by a former drainage ditch (Figure 2.3). The western half of the site was an arable field sloping from 1.9 m - 2.4 ODN (4.6 – 5.1 m CD), into terrestrial habitats (Jain 2004). It has developed a diverse zonation of structurally complex saltmarsh vegetation and associated marine invertebrate saltmarsh fauna (Colclough et al. 2005). The maximum time available for fish to feed at the bottom of this half of the site on a spring tide would be approximately three hours. The average fish feeding time in the sloping field is approximately two hours, based on an average elevation of 4.85 m CD. The eastern half of the site is below MHWNTL, largely unvegetated, and contains ditches and an old decoy pond which receives some freshwater from a pond to the north (Figure 2.3). The fish feeding time on a spring tide would be delayed because of the elevated access point through breach C. Therefore the maximum time would be approximately three hours, when, in contrast to the western half, most of the site would be immersed.

The established saltmarsh creek leading to breach C was also fished on the flood tide close to Salcott channel, and on the ebb tide higher up where the water had not mixed with that leaving the managed realignment site (Figure 2.3). This complex established saltmarsh is largely a plateau at 4.3-4.7 m CD but vegetation lies between MHWNTL and MHWSTL (450-500 tidal inundations per year) and the creeks lie below MHWNTL. On a spring tide, the fish have approximately four hours to feed in the creeks and two hours in the vegetation.

Figure 2.2: An aerial photograph of Abbotts Hall before the managed realignment. The letters show the position of the five breaches (A-E) in the seawall. The blue areas represent the extent of tidal inundation of the managed realignment on high spring tides. The white box marks the area of fishing shown in Figure 2.3

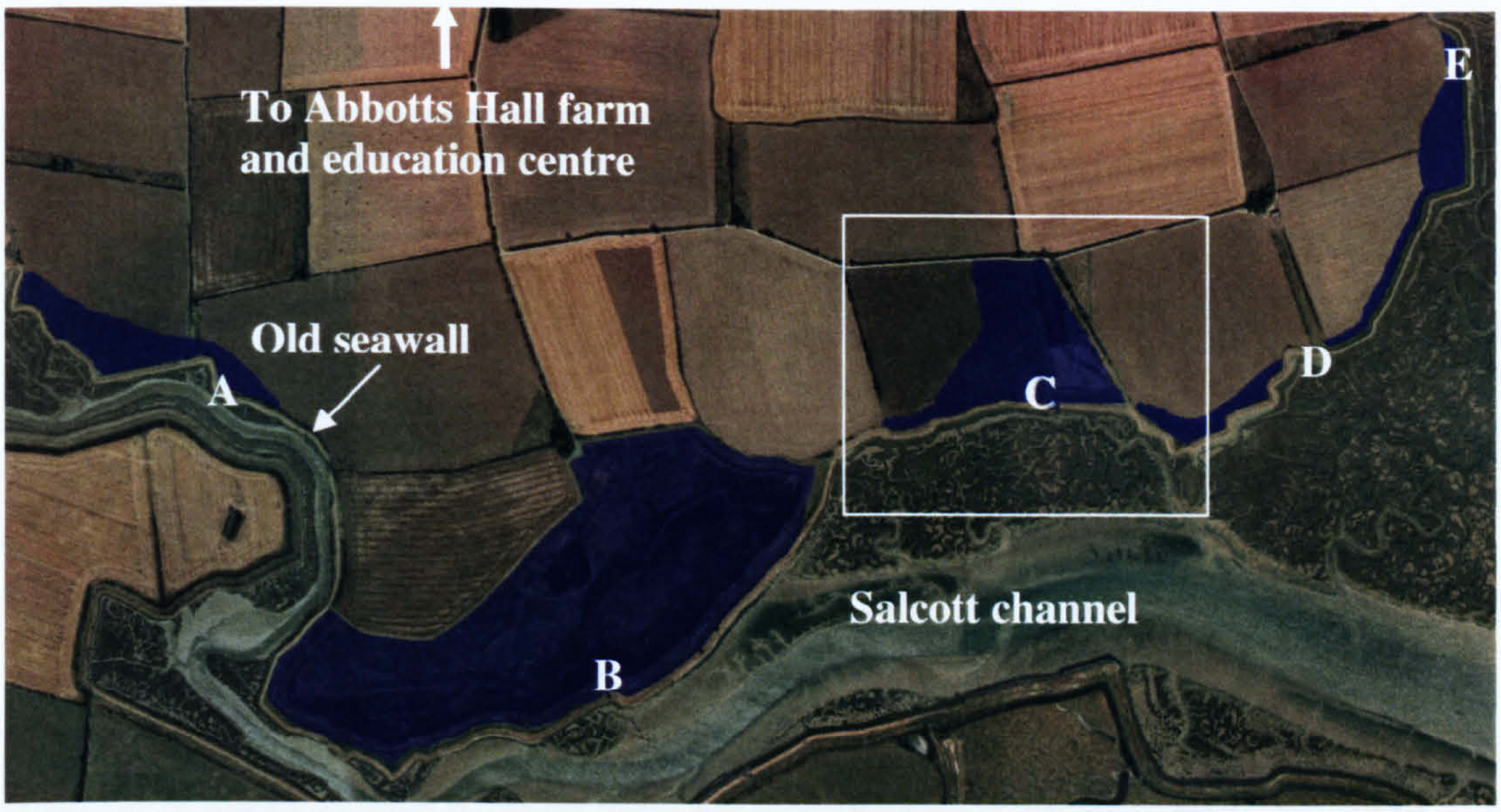

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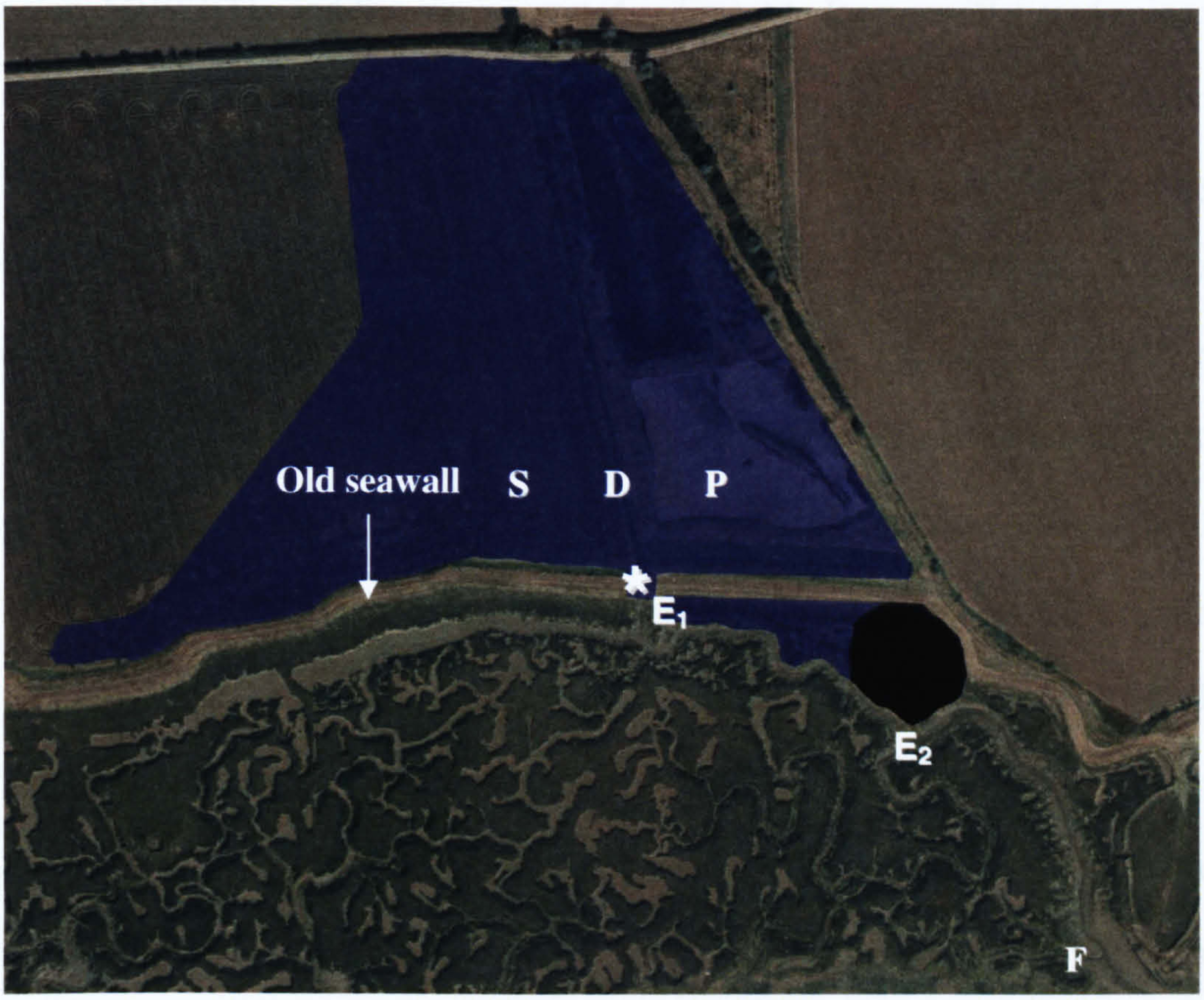
Figure 2.3: An aerial photograph of the sampling areas around breach C (*) at Abbotts Hall. Also shown are the locations of the static seine net sampling in 2004-2006 of the flood tide (F); the ebb tide from the managed realignment (E_1); and the established saltmarsh (E_2). The black area marks the 0.1 ha of saltmarsh fished quantitatively (at E_1) in 2007. The sloping field, decoy ponds and drainage ditch are marked 'S', 'P' and 'D' respectively



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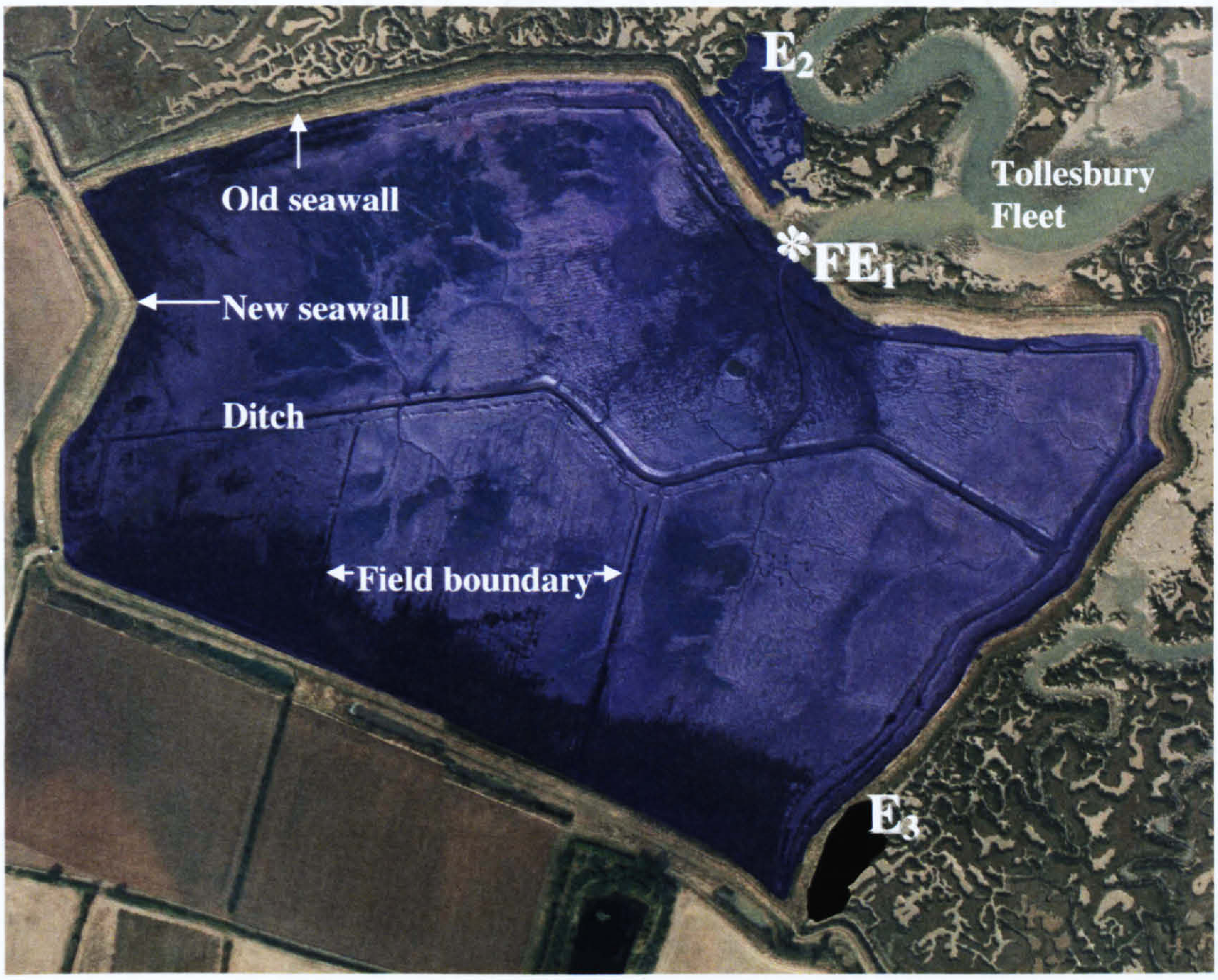
Tollesbury

The Tollesbury realignment site is located on Tollesbury Fleet, a tributary of the Blackwater Estuary. It is 21 ha and the single 40 m breach was created in August 1995 (Watts et al. 2003). Before breaching, the site was heavily compacted arable land mostly below MHWNTL, and has since accreted sediment to form mudflat predominantly and an associated benthic marine invertebrate community (DEFRA 2004; Paramor and Hughes 2005). At Tollesbury (West Mersea), MHWNTL was at approximately 1.6 m ODN (3.8 m CD) and MHWNSTL was at approximately 3 m ODN (5.1 m CD) (Watts et al. 2003; Paramor and Hughes 2005). The majority of the site lies below 2 m ODN (4.16 m CD). At MHWNTL, 15 of the 21 ha are flooded, and during MHWSTL, the whole site, including the 6 ha of developing saltmarsh, is flooded (Garbutt et al. 2002; Watts et al. 2003; Wolters et al. 2005). The site is dissected by a former irrigation ditch that was connected to the breach (Figure 2.4). The realignment area is bounded by the borrow dyke on the inside of the old sea wall. The ditches and dykes may provide access for fish to the higher vegetated parts of the site. Mean tidal immersion durations range from 45 % at 1.0 m ODN to 15 % at 2.5 m ODN (Watts et al. 2003) and on a spring tide the fish would have a feeding time of approximately four hours based on the average habitat elevation. Flood tide fish samples were collected from within the breach as were the ebb tide samples from the realignment.

The established saltmarsh adjacent to Tollesbury managed realignment area has a similar elevation and landscape structure to the established marsh adjacent to Abbotts Hall managed realignment area. Thus on a spring tide, the fish have approximately four hours to feed in the creeks and two hours to feed within the vegetation on the plateau. The fish were collected on the ebbing tide from a creek where the water had not mixed with water leaving the managed realignment area (Figure 2.4).

Figure 2.4: An aerial photograph of Tollesbury managed realignment site. The blue area represents the extent of tidal inundation of the realignment area and established saltmarsh sampled on high spring tides. The locations of the static seine net sampling in 2004-2006 of the flood tide (F) and the ebb tide from the managed realignment (E_1), in the breach of the seawall (*), and the saltmarsh (E_2) are shown. The black area shows the 0.1 ha of saltmarsh that was fished quantitatively (at 'E_3') in 2007



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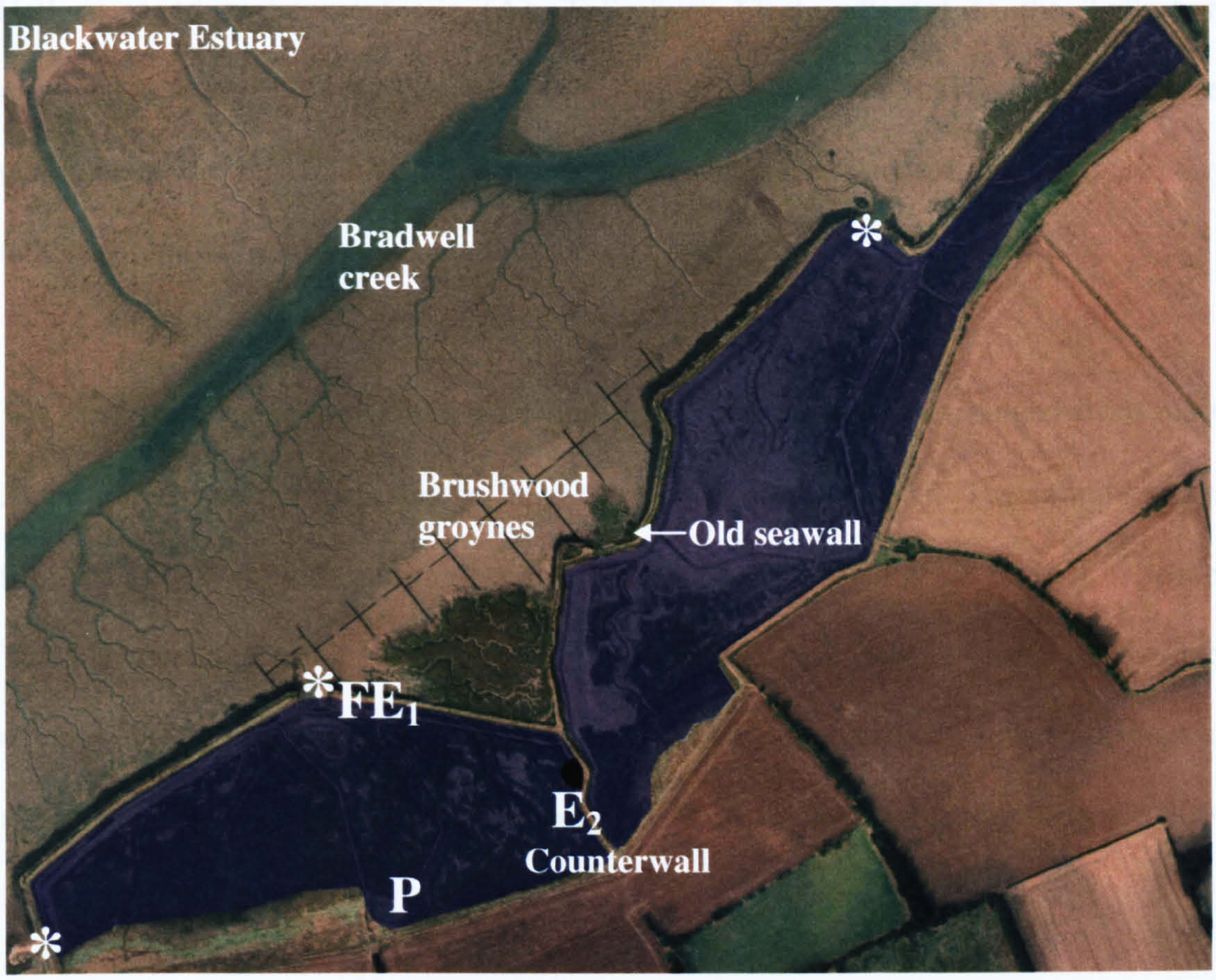
Orplands

The Orplands managed realignment area is 38 ha, and was formed in 1995 (Figure 2.5). It is located on the Dengie peninsula, half a mile west of Bradwell Marina. At Orplands (Bradwell Waterside), MHWNTL is at 1.5 m ODN (4.2 m CD) and MHWNSTL was at approximately 2.7 m ODN (5.3 m CD). Orplands was originally higher than Tollesbury and pioneer zone saltmarsh vegetation has developed over most of the site except in some low-lying basins that accreted sediment and remain as mud (Paramor and Hughes 2005).

The mean height of the site is 2.6 m ODN (5.2 m CD) ranging from 1.3 to 3.8 m ODN (3.9 - 6.4 m CD) (DEFRA 2004). The site is split in half by a counter-wall, and the western half was sampled during this study (Figure 2.5). The sampled area mainly comprises pioneer zone saltmarsh (Spencer et al. 2008) intersected with steep sided linear creeks, dug to establish a drainage system extending to a permanent saline pool at the top of the site (Figure 2.5). The elevation of the creeks and saltmarsh sampled is 0.5 - 4.0 m ODN (ABPMer 2008). The feeding time of fish on a spring tide is on average four hours in the creeks and less than one hour over the vegetated flat.

Figure 2.5: An aerial photograph of the Orplands managed realignment site. The asterisks mark the three breaches in the seawall. The blue layer represents the area of tidal inundation. The locations of the static seine net sampling in 2004 - 2006 on the flood tide (F) and the ebb tide from the managed realignment (E_1) are shown. The black area represents the 0.1ha of saltmarsh that was fished quantitatively in 2007 (E_2). The location of the permanent saline pool is shown (P).



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Environmental Parameters

Some environmental parameters were measured every two months by the Environment Agency from a boat at high tide between June 2004 and October 2007 from three sites on the Blackwater Estuary. The sites are: the Salcott Channel adjacent to the Abbotts Hall managed realignment site (A); Tollesbury Fleet, adjacent to the Tollesbury managed realignment site (T); and Bradwell creek adjacent to Orplands managed realignment site (O). The parameters measured were: water temperature, pH, salinity, total chlorophyll, transparency, and dissolved oxygen.

The data are presented in Figures 2.6 and 2.7. Water temperatures ranged from 3.3 to 21.0 ^{o}C with minima occurring in January and maxima in August. The salinity ranged from 29.3 to 35.3, with minima occurring during periods of highest rainfall in winter. The pH remained stable throughout the sampling period. Spring peaks in dissolved oxygen concentrations, high chlorophyll concentrations and low transparency (turbidity), were consistent with the occurrence of an annual algal spring bloom in 2004, 2005, 2006.

Figure 2.6: Water temperature (^{o}C), pH, and salinity (June 2004 - October 2007) at Salcott Channel adjacent to Abbotts Hall (●); Tollesbury Fleet (▼); and Bradwell creek adjacent to Orplands (o). The data was provided courtesy of the Environment Agency

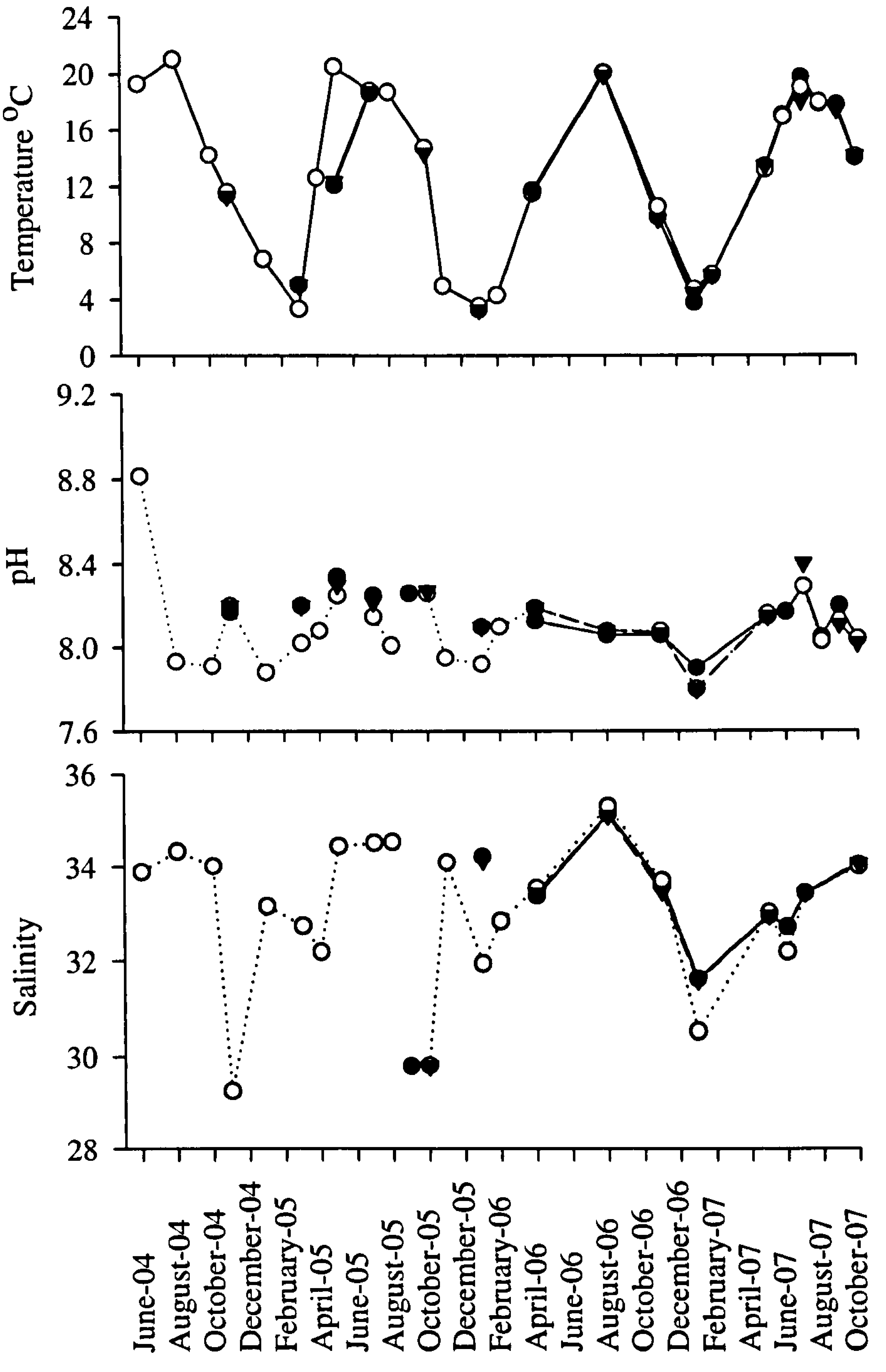
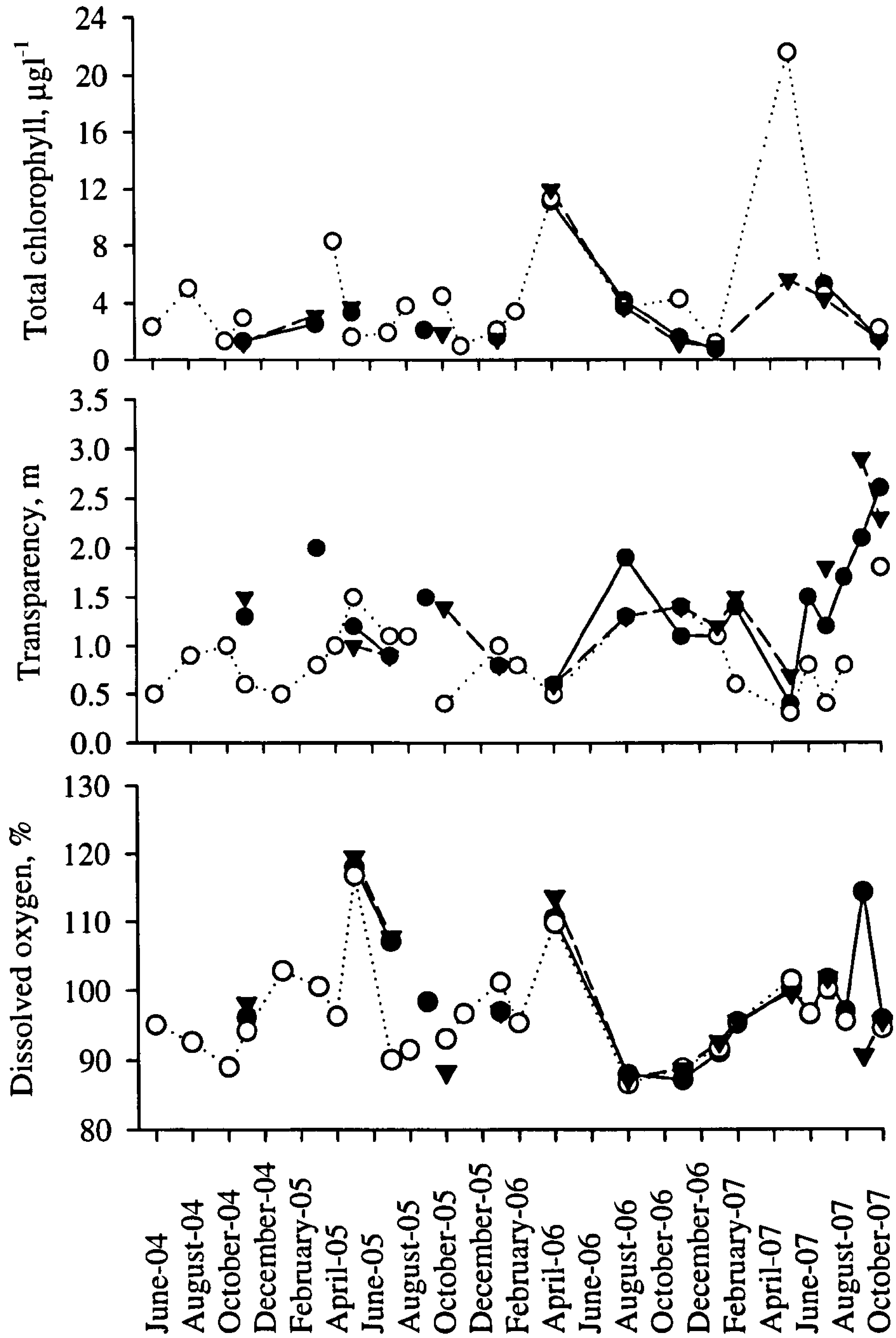


Figure 2.7: Total chlorophyll (μg l^{-1}), transparency (m), and dissolved oxygen (%) (June 2004 - October 2007) at Salcott Channel adjacent to Abbotts Hall (●); Tollesbury Fleet (▼); and Bradwell creek adjacent to Orplands (o). The data was provided courtesy of the Environment Agency



Methods of fish collection

Saltmarsh creeks are important corridors between subtidal and intertidal habitats (Desmond et al. 2000; Paterson and Whitfield 2000). Creek fishing in saltmarshes was first carried out in various USA states such as North and South Carolina (Shenker and Dean 1979b; Bozeman and Dean 1980; Hettler 1989); Virginia (Weinstein and Brooks 1983; Rozas and Odum 1987); Georgia (Kneib and Wagner 1994); New Jersey (Able et al. 2005); and Delaware (Rozas and Odum 1987; Kneib and Wagner 1994; Able et al. 2003; Nemerson and Able 2003; Teo and Able 2003); as well as more recently in South Africa (Paterson and Whitfield 2000); South Australia (Connolly 1994; Bloomfield and Gillanders 2005); and Italy (Franco et al. 2006) where the creeks typically retain some water at low tide.

In contrast, creek fishing in the UK (Colclough et al. 2005), France (Lefeuvre et al. 1999; Laffaille et al. 2000; Laffaille et al. 2001a), Spain (Drake and Arias 1991), Portugal (Cabral and Costa 2001; Salgado et al. 2004a; Salgado et al. 2004c), and Belgium (Cattrijsse et al. 1994) has included macrotidal areas, where the creeks dry out at low tide. Fish in drying creeks potentially have longer tidal migration routes and shorter feeding times in the creeks (Cattrijsse and Hampel 2006).

Fish collection for dietary comparison

A number of fishing techniques were considered, and tested, in order to collect a representative sample of fish of varied sizes and in sufficient numbers for quantitative comparisons of their diets. The techniques consisted of passive and active methods previously used to collect fish in European saltmarshes and creeks (Aprahamian and Barr 1985; Kelley 1986; Hettler 1989; Lancaster 1991; Connolly 1994; Duffy-Anderson et al. 2003; Colclough et al. 2005).

Methods considered and not used

A 10 m x 1 m knotless, floated and weighted seine net (5 mm mesh), was pulled through the saltmarsh creeks (Figure 2.8) but the action of pulling it caused the ground rope line to lift off the bottom, allowing fish to escape.

A 35 m x 2 m seine net with floats and a lead line (5 mm mesh in the cod end and 10 mm mesh wings) was tested but was too large to be used in the creeks.

A 3 m x 1 m push net (4 mm mesh) was also used but was not successful in the narrow creeks and could only be used on vegetated flats when there was no strong current (Figure 2.9).

A rectangular fyke net (2.5 m long x 0.5 m high x 0.4 m wide, with two 5 m long x 30 cm high wings, 4 mm knotless mesh, 1 mm knotless mesh in the weighted cod-end) was staked into creeks and the breaches of the realignment sites at low tide (Figure 2.10). The intention was to provide a regular semi-quantitative sample for seasonal comparisons of abundance. However, in general the catches were low and fish not associated with the creek bed may have been underrepresented (e.g. few sand smelt were collected). Further, the fish could not be retrieved and frozen soon enough after capture to halt digestion of small prey items.

Figure 2.8: Seine net (10 m x 1 m) used at Abbots Hall managed realignment site, 2004

Figure 2.9: Push-net used at Abbotts Hall managed realignment site, 2004

Figure 2.10: Fyke net staked in breach C at Abbotts Hall managed realignment site, 2005

Although a combination of the methods described above would be appropriate for sampling estuarine fish communities (Butcher et al. 2005; Colclough et al. 2005), their high catch unpredictability made them unsuitable for dietary studies, therefore it was decided to use the static funnel method described below.

Static-funnel net

A 2 m x 2 m x 3 m deep static-funnel net (4 mm mesh, 2 mm mesh cod end) was designed specifically for use in these creeks of varied depth (Figure 2.11). It had an internal funnel (1 m deep, 4 mm mesh) stitched into the 2 m x 2 m mouth, to guide fish towards the cod-end, with an aperture of 9 cm to help to prevent them from escaping backwards through the mouth. Three 2 kg weights were attached to the base of the net to stop fish swimming underneath it. As the water depth and creek shape changed with the tide, six side-ropes (attached to the top, middle and bottom of both sides of the mouth) were used to adjust the net height and width to keep the net flush with the creek sides (Figure 2.11). This design was similar to the 'channel' net used by Bozeman and Dean (1980) in marshes in South Carolina, being large enough to reduce the chances of producing results due to small-scale patchiness but small enough to be portable. If the flow through the creeks was slow or static, the net was pulled from both creek banks; however, the catches were higher when it was used passively in faster flowing water. It was deployed across the flooding and ebbing tides, in suitable creeks for a standardised unit of effort of 30 minutes after which time the fish catch was retrieved and frozen. The static-funnel method has similar benefits to a lift net (Rozas 1992), as it causes minimal habitat disturbance and can be deployed in very small creeks.

On the flooding tide, the catches were greatest as the creeks filled, but once the tide reached the saltmarsh plateau, the proportion of the tide flowing through the creeks was severely reduced, which may have contributed to the marked decline in catches (Rozas and Minello 1997). For this, and for safety reasons, the regular catches were made only as the creeks were filling and emptying.

Figure 2.11: Static funnel net set in an eroding established saltmarsh creek, 2005. This was the preferred method for semi-quantitative sample collection. The position of the top left-hand side-rope is shown (S).

In the trials, the catches were highest when the net was placed to fish the earliest stages of the flood tide (personal observation). This trend of fish accessing the marsh in shallow water at the front of the tide, has also been observed in some US saltmarshes (Rozas 1995) and in Europe (Cattrijsse et al. 1994). Cattrijsse et al. (1994) observed most fishes migrating during the first and last hours of the tide when tidal currents were slowest, and suggested that these movements were active in part. This may be because juvenile fishes are attracted to turbidity maxima, such as those at the sediment-water interface at the shallow front of the flooding tide, because the fishes encounter more prey (Rothschild and Osborn 1988; Hibino et al. 2006; Islam et al. 2006), predation by visual predators is reduced (Shoji and Tanaka 2007), and larger predators are less abundant (Parrish 1989). Therefore the flood tide fishing effort was focussed on the earliest tidal stages. The ebb tide fishing effort began as soon at the saltmarsh plateau was emersed and the nets could be placed in the creeks. In all cases, fishing was conducted for 30 minutes for analysis of the fish community. For the purposes of gut contents analysis, the fish were removed from the net and the fishing was then continued in further 15 minute periods until at least ten fish were collected.

Sampling was standardised where possible to ensure that the data reflected actual changes in the populations and communities (Allen et al. 1994). Samples were collected during high spring tides because the creeks would fill completely (and then flood the saltmarsh) and the currents were relatively fast (at around mid tide), consequently the nets were more effective. On neap tides, the creeks do not fill completely and the flows are slow, as the rising water is closer to high water. Furthermore, fish do not have access to all the saltmarsh habitats on neap tides, and their diets would be restricted by the low level of high tide. Reduced saltmarsh access on neap tides may allow the accumulation of food resources which then become available to fish on spring tides. For example in the US, Gulf Killifish, *Fundulus grandis* ingest up to eight times more food by weight on spring tides than at other stages in the lunar cycle (West and Zedler 2000). Fish also have additional prey types available to them on spring tides. These include insects and spiders associated with the vegetation and talitrid amphipods found at the strandline not reached by neap tides.

Nocturnal tides were not sampled because of health and safety issues and because the gut fullness of 0-group bass caught in saltmarshes has been found to be significantly lower during nocturnal tides (Cabral and Costa 2001). Also Hibino et al. (2006) found that juvenile Japanese bass, which are visual zooplanktivores, stop feeding during the night altogether.

Quantitative estimates of fish abundance

The use of the static-funnel net in shallow water consistently provided sufficient numbers of fish from each sampling event for gut contents and stable isotope analyses. Although passive methods should generally be used to collect fish, rather than to sample saltmarsh fish assemblages (Rozas and LaSalle 1990; Layman and Smith 2001), the net was positioned in a focussed flow to provide a semi-quantitative estimate of the fish community. However, smaller individuals, or species associated with the shallowest water, such as 0-group bass and small adult gobies, may have been positively selected for with this method. Also, the net was not deployed in a closed system over whole tides so did not provide a fully quantitative sample. Therefore in 2007 a second and quantitative method was used to assess relative abundance of fishes.

A spatial comparison of the saltmarsh fish assemblages was conducted by quantitatively sampling three enclosed 0.1 hectare areas of saltmarsh and creeks in July and August 2007. Approximately semicircular areas of marsh, each fed by one feeder creek and already partly enclosed by an adjacent sea wall, were enclosed to a height greater than that of high tide, with a fixed block net (70 m long x 2 m tall, 4 mm mesh, floated and weighted), except for the feeder creek. In the feeder creek, a collapsible static-funnel net (2 m x 3 m x 6.5 m deep with two 3 m x 2 m wings, 4 mm mesh, and 2 mm mesh in the cod-end) was secured to the creek bottom, and weighed down to prevent movement with the incoming tide and to allow unrestricted access of the fish (Figure 2.12). Fish could only access the enclosed area to be sampled by this feeder creek route because the perimeter block-net prevented access to the sampled area by fish that swim over the vegetation (Figure 2.13).

At high water, the weights were removed from the collapsible static-funnel net. The net was raised carefully to the level of the water and the head rope was attached to a floated line already in position (Figure 2.13). Every attempt was made not to disturb the water between the flood and ebb tides, and it was assumed that no fish left the enclosed area before the net was raised at the time of high water. Although some fish may have been lost through predation, catches of large (bigger than 1-group) bass and crabs were rare, and no piscivorous birds were in the vicinity at the time of sampling.

Figure 2.12: Collapsible static-funnel net deployed for the first time with the help of Environment Agency staff. The net was deployed in a feeder creek within the established saltmarsh adjacent to Tollesbury Managed Realignment, 2006

Figure 2.13: The raising of the collapsible static-funnel net at high tide in Orplands managed realignment, 2007. The positions of the feeder creek (F) adjacent to the seawall (S), the collapsible static-funnel net (C) and the semicircular fixed perimeter block-net (dotted blue line) delimiting the 0.1 ha of saltmarsh sampled, are shown (photo courtesy of Jan Domke).

Since no fish were found stranded on the vegetated plateau by the block net it is assumed that the fish leave the area via the creek system and hence all fish doing so would have been caught. When the cod end was emersed, it was emptied of fish, and the fish caught were killed. The identity and fork length of every fish was then recorded in the laboratory. This method was repeated over the next two days at the same site.

This more labour-intensive fishing method was of a type described as a 'lift', 'pop' or 'modified-block' net method (Larson et al. 1986; Hettler 1989; Connolly 1994). Unlike the static funnel, the collapsible static-funnel method rules out sampling bias, as fish which might be more or less attracted to specific microhabitats such as newly submerged marginal vegetation, would all be forced into the net as the tide receded (Peterson and Turner 1994; Rozas and Minello 1997). Sampling was carried out in the established saltmarshes adjacent to the Abbotts Hall and Tollesbury managed realignment sites, and within the Orplands managed realignment site. Saltmarsh areas with complex and extensive creek systems were chosen to ensure the water flows were moderate, to prevent the net becoming dislodged, but sufficient to allow the fishing of a substantial area of saltmarsh.

At each of the three sites, samples were collected on three consecutive daylight spring tides in July and August 2007. These summer spring tides had an 'intermediate' spring tide range with the heights between 4.5 and 5.3 m above chart datum. These tides were chosen for three reasons. Firstly, in previous trials conducted on neap tides below 3.8 m high tide, bass were not caught (personal observation). Secondly, on high spring tides above 5.5 m the water level was higher than the block nets, therefore some fish could escape. Thirdly, these three consecutive spring tide periods had a low variation in their heights (70 cm) reducing the temporal variation between them.

Chapter 3: Composition and seasonal fluctuations in the fish assemblages of saltmarsh habitats within the Blackwater Estuary

Introduction

Saltmarshes provide important refugia and feeding habitats for a range of resident and marine fishes, including those of commercial importance (Shenker and Dean 1979a; Drake and Arias 1991a; Cattrijsse et al. 1994; Costa et al. 1994; Viega et al. 2006). These habitats improve recruitment success by increasing the growth and survival of postlarvae and early juveniles which tend to use deeper water with increasing size (Weinstein and Brooks 1983; Rothschild 1986; Baltz et al. 1993). The abundance, composition and size structure of fish assemblages in saltmarshes is influenced mainly by seasonal variations in recruitment periods; abiotic conditions such as salinity, water temperature and turbidity, as well as the habitat type (Blaber and Blaber 1980; Brunton 1985; Drake and Arias 1991a; Akin et al. 2003; Martinho et al. 2007). Fish catches are affected by the sampling methods and equipment and the scales used in the analysis of the data (Methven et al. 2001).

The majority of fish studies in saltmarshes have been conducted in North America (see Chapter 2). Mostly, these saltmarshes have smaller tidal ranges than European ones and the creeks often contain permanent water, and hence the fish populations are easier to study (Cattrijsse et al. 1994; Colclough et al. 2005; Cattrijsse and Hampel 2006). In contrast many North Western European saltmarshes, including those in S.E. England, experience relatively high tidal ranges and are immersed fully only during high spring tides (Laffaille et al. 2000). The saltmarsh creeks dry out at low tide and, in the absence of permanent water bodies, fish can only access the creeks for short periods of time. For example, in the Mont Saint-Michel Bay, France, Laffaille et al. (2001a) reported that fish could only access the saltmarsh creeks for 43 % of the tides, and that they could only access the vegetated flats for 5-10 % of the tides, and then for only 1-2 hours. However, in a review comparing US and European estuaries containing saltmarshes, European habitats contained a higher species richness per system than those in North America (Nordilie 2003).

European saltmarsh fish assemblages are generally dominated by a lower number of species than those in North America. For example in Cadiz Bay saltmarshes, Spain, Drake and Arias (1991a) reported 39 fish species and in the Mont Saint-Michel Bay saltmarshes (Laffaille et al. 2000) recorded 31 fish species. Despite taxonomic, physical and chemical differences, European saltmarshes are often characterised by a high abundance of estuarine residents such as species belonging to the Gobiidae family, as well as juveniles of marine species (Mathieson et al. 2000; Hampel and Cattrijsse 2004). Fishes commonly encountered within the Greater Thames Estuary include: *Pomatoschistus microps, Pomatoschistus minutus*, *Aphia minuta, Anguilla anguilla*, *Clupea harengus*, *Sprattus sprattus*, *Sardina pichardus*, *Engraulis encrasicolus*, *Syngnathus rostellatus, Syngnathus acus*, *Atherina presbyter*, *Liza ramada*, *Dicentrarchus labrax*, *Platichthys flesus*, *Pleuronectes platessa*, and *Solea solea* (Andrews 1984; Colclough et al. 2002; Elliott and Hemmingway 2002).

The majority of the research relating to the fishes of the Greater Thames Estuary (which includes the estuaries of the Essex coast) focussed on the subtidal habitats of the tidal Thames (Wheeler 1979; Andrews 1984; Alabaster and Gough 1986; Naismith and

Knights 1990; Araujo et al. 1998; Thomas 1998; Araujo et al. 1999; Colclough et al. 2000; Power et al. 2000; Attrill and Power 2002; Colclough et al. 2002; Power and Attrill 2007; Leakey et al. 2008). The published literature on the fish populations of the Blackwater Estuary relate predominantly to the tagging of juvenile (predominantly 3-group), adolescent, and adult bass (Pickett and Pawson 1994; Pickett et al. 1995; Pawson and Pickett 1996; Pickett et al. 2004) and the larval and juvenile stages of herring *Clupea harengus* (Dempsey and Bamber 1983; Henderson et al. 1984; Henderson 1987; Fox et al. 1990; Fox et al. 1999; Fox 2001). The presence of the rock goby *Gobius paganellus*, and the two spot goby *Gobiusculus flavescens* in the Blackwater Estuary has also been recorded (Barron 1974).

Many writers have investigated the value of UK estuaries to fish (Aprahamian and Barr 1985; Pomfret et al. 1988; Kelley 1988a; Elliott and Taylor 1989a; Lancaster 1991; Jennings and Pawson 1992; Colclough et al. 2002; Coates et al. 2007). The Blackwater estuary, in SE England, is designated a 'Site of Special Scientific Interest' and a 'Special Protected Area' (see Chapter 2 for a physical description of the Blackwater Estuary). The estuary supports a number of commercially important fishes, including *Sprattus sprattus*, *Clupea harengus*, *Solea solea*, *Gadus morhua*, *Merlangius merlangus*, *Platichthys flesus*, *Atherina presbyter*, *Chelon labrosus*, and *Dicentrarchus labrax* (Chesman et al. 2006).

The Centre for Environment, Fisheries, and Aquaculture Science (CEFAS), conduct annual autumn beam trawl fish surveys in the Blackwater Estuary. Two additional subtidal monitoring surveys were conducted in June and September 2006 by the Environment Agency (EA) as part of a larger project to classify all transitional water bodies for compliance with the EU Water Framework Directive. A summary of the combined CEFAS and EA subtidal 2006 catch data from the marine zone of the estuary (Tollesbury Spit, Mersea Is., and Bradwell beach) using a combination of beam and otter trawls, fyke nets, and seine nets, is provided in Table 3.1. Intertidal areas such as saltmarshes have not been included in the Blackwater estuary surveys, because of a lack of awareness of their potential value, difficulties in sampling (Colclough et al. 2005) and in the accurate identification of larvae and juveniles.

Aims

The aims of the study were to determine:

a) which fish species use the saltmarshes and managed realignment areas, which functional guilds they belong to,

b) the temporal variations in the relative abundance and size structure of the fishes, including the growth rate of bass *Dicentrarchus labrax* (February 2006 - January 2007)

c) the absolute abundance and densities of fishes (July and August 2007).

Table 3.1: The Blackwater Estuary subtidal fish community composition (Tollesbury spit, Mersea Is., and Bradwell beach) 2006 using trawls, fykes and seine nets. The species in each guild were listed alphabetically according to family. Species marked with an asterisk were also collected in the saltmarshes. The data were provided courtesy of the Environment Agency

			Spring (June)			Autumn (Oct & Nov)		
Ecological guild	**Family**	**Species**	**n**	**Length range, mm**	**Mean length, mm ± SD**	**n**	**Length,mm range**	**Mean length, mm ± SD**
Marine straggler	Agonidae	*Agonus cataphractus* (L.)				11	45-95	67 ± 16
	Callionynidae	*Callionymus lyra* (L.)				1	60	
	Clupeidae	*Sprattus sprattus* (L.)*	29	30-52	41 ± 5	58	35-83	52 ± 10
	Gadidae	*Gadus morhua* (L.)				6	185-415	288 ± 96
		Merlangius merlangus (L.)				13	135-325	260 ± 53
		Trisopterus luscus (L.)				2	235	235 ± 0
	Lotidae	*Ciliata mustela* (L.)				3	96-185	132 ± 47
	Mugilidae	*Chelon labrosus* (Risso)				6	19-33	27 ± 5
	Triglidae	*Chelidonichthys lucerna* (L.)	2	85-117	101 ± 23	4	165-375	263 ± 87
	Zoarcidae	*Zoarces viviparus* (L.)	1	180				
Marine estuarine dependent	Atherinidae	*Atherina presbyter* (Cuvier)*	29	30-124	48 ± 21	8	58-73	67 ± 5
	Clupeidae	*Clupea harengus* (L.)*				2	215-255	235 ± 28
	Pleuronectidae	*Pleuronectes platessa* (L.)	2	45-55	50 ± 7			
	Serranidae	*Dicentrarchus labrax* (L.)*	2	240-302	271 ± 44	11	81-251	123 ± 61
	Soleidae	*Solea solea* (L.)	5	93-109	104 ± 7	1	75	
Estuarine Resident	Gobiidae	*Aphia minuta* (Risso)*	2	50-60	55 ± 7			
		Pomatoschistus microps (Krøyer)*				3	30-41	36 ± 6
		Pomatoschistus minutus (P.)*	9	40-70	56 ± 9	20	28-73	46 ± 12
	Pleuronectidae	*Platichthys flesus* (L.)*				1	194	
	Syngnathidae	*Syngnathus acus* (L.)*	1	132		1	81	
Diadromous	Anguillidae	*Anguilla anguilla* (L.)				1	395	

Methods

Community composition

To assess the seasonal variations in the relative abundance of fishes using the saltmarsh habitats, fishes were collected on daylight ebb spring tides, from the realignment sites at Tollesbury, Orplands and Abbotts Hall. At each site, one sample was taken each lunar month (four weeks), which also corresponded to calendar months, between February 2006 and January 2007. The fish were caught using a static-funnel net, held across creeks. In each case, the fishing effort was standardised to 30 minutes to allow comparisons between collections. See Chapter 2 for details of the sites, fishing methods and environmental parameters.

Quantitative assessments

A quantitative assessment of the abundance of fishes in three habitats was conducted in summer 2007. The three habitats were within one restored saltmarsh (Orplands managed realignment area) and two ancient saltmarshes adjacent to Tollesbury and Abbotts Hall realignment. See Chapter 2 for details of these sites and fishing methods. The length from the nose to the fork in the tail of each fish was measured. Three replicate samples were collected at each site on successive days in July and August, 2007.

Species identification

All fishes were identified to species. In most cases this was straightforward but differentiation between *Liza ramada,* and *Liza aurata* (and *Chelon labrosus*, which was not caught), required the use of a combination of the number and shape of the pyloric caeci, the melanophore pattern on the ventral side of the head and the expected length according to the expected spawning season and their growth rate (Reay and Cornell

1988). Older *Liza aurata* juveniles also had a golden spot on their operculum. Small *Sprattus sprattus* and *Clupea harengus* were identified using the number of pyloric caeci because external features, such as the relative position of the ventral and dorsal fins, and serrations on the ventral side, are indistinguishable in small fish. *S. sprattus* has seven pyloric caeci, and *C. harengus* has 18-23 (Hayward and Ryland 2004).

Fishes were allocated to four functional ecological guilds described by Elliott and Hemmingway (2002). These were: 'diadromous' fish which use the estuary or an estuarine habitat as a migration route for spawning; 'estuarine resident' fish which breed in the estuary; 'marine estuarine dependant' fish which use estuaries as juveniles; and 'marine straggler' fish which infrequently enter estuaries.

Data analyses

Length frequency histograms were constructed for all species but there were only sufficient data from consecutive months for analysis of 0-group *D. labrax* growth rates. The instantaneous growth rate (% total length increase per day) of 0-group bass was calculated for four time periods (July to August, August to September, September to October and December to July) according to the formula below (after Lancaster 1991) which assumed that the cohort mean length was unaffected by continuing recruitment in July or the loss of larger fish by migration later in the year:

$$G = ((\log_e L_T - \log_e L_t) / T\text{-}t) \times 100 \qquad \textbf{(3.1)}$$

where L_t = total length at initial time, t

L_T = total length at final time, T

The temporal variations in the fish abundance were analysed using $\log_{10}(x + 1)$ transformed data. Multivariate analyses used were ANOSIM, cluster analysis, and covariance Principal Components Analysis (Community Analysis Package 3.0 software © PISCES Conservation Ltd). There were no significant differences in the number of each species caught each month between the three sites (ANOSIM $P > 0.05$), therefore the fish abundance data from the three sites were combined. A cluster analysis was performed (Ward's methods, Euclidean distances) to determine if the monthly collections exhibited a seasonal pattern (Field et al. 1982; Laffaille et al. 2000) and covariance principal components analysis was used to identify the similarities between the monthly collections. Non-metric multidimensional scaling was attempted (PcORD © MjM Software) to determine the relationship between the environmental parameters measured by the Environment Agency (see Chapter 2) and the saltmarsh fish community. However the NMDS could not be performed because a reliable co-ordination solution to the data was not found: the best solution was with one axis, which represented 69% of the data but the stress value was unreliable at 0.25.

The spatial variations in the abundance and biomass of fishes caught using the quantitative method in July and August 2007, were analysed using ANOVA.

Results

Community composition

In total, 10,798 fishes from eight families and 14 species were collected during the two sampling campaigns (Tables 3.2 -3.5). Three species were marine stragglers, four were marine estuarine dependants, five were estuarine residents, and two were diadromous. Of the 21 species found in the subtidal regions of the Blackwater Estuary in 2006, nine were also collected in the saltmarshes (Table 3.1). Four species collected in the saltmarsh were not collected subtidally. These were 92 *Liza ramada* and 112 *Liza aurata,* nine *Sparus aurata* and one *Entelurus aequoreus.*

Between February 2006 and January 2007, 761 fishes belonging to 8 families and 13 species were collected (Table 3.2). Figure 3.1 shows the length frequency of all the fishes caught. The 'marine estuarine dependent' group dominated the catches in biomass (85.2 %), and frequency of occurrence (47.9 %), but fishes of the 'estuarine resident functional' group were the most abundant (41.0 %) because of the high abundance of species belonging to the Gobiidae family (see below) (Table 3.2). The Gobiidae was the most abundant family, comprising 36 % of the catch, followed by Mugilidae (20 %) and Serranidae (19 %) (Table 3.2). Six species (*Atherina presbyter, Sprattus sprattus, Liza aurata, Liza ramada, Dicentrarchus labrax,* and *Pomatoschistus microps*) represented 94 % of the total abundance (Table 3.2). The most abundant species were the estuarine resident *P. microps* (35.7 %); and the marine dependent *D. labrax* (19.3 %) both of which occurred frequently ($\geq$ 50 % frequency of occurrence) (Table 3.2). The overall biomass was dominated by *D. labrax* (72.3 %) (Table 3.2 and Table 3.4). The size frequency data (Figure 3.1) indicate that most individuals were 0-group; however some older *D. labrax, A. presbyter* and *P. microps* individuals were also caught (Table 3.4 and Figures 3.1).

Growth rates of 0-group bass

Two 0-group cohorts of bass were collected in the saltmarshes in 2006 (Figure 3.1). The first group (length 5 cm) appeared in May and may have been spawned offshore in February (see Discussion). The second cohort appeared in July and the growth rates of this cohort were estimated to be 1.85 % d^{-1} between July and August; 1.54 % d^{-1} between August and September; 0.44 % d^{-1} between September and October and 0.56 % d^{-1} between October and December. Growth was lowest between December 2006 and July 2007 (0.28 cm d^{-1}).

Temporal trends in the community

Overall there was a strong seasonal trend in the abundance and biomass throughout the year (Figures 3.1, and Tables 3.3, and 3.4). The cluster analyses revealed three main groups on the basis of monthly numerical abundance (Table 3.3 and Figure 3.2). The groups were a) February to April 2006, dominated by *P. microps* and *S. sprattus* b) May to September 2006 characterised by *D. labrax*, *P. microps* and *A. presbyter* and c) October 2006 to January 2007 dominated by *L. aurata* and *L. ramada* (Table 3.3 and Figures 3.2 and 3.3).

P. microps was the only species present in February and March, and by April there were increased numbers of *S. sprattus* and *P. microps* (Table 3.3). The 'May - September' group was separated into two sub-groups (Figure 3.2). Firstly, a recruitment period occurred between May and June with the appearance of several species, particularly *D. labrax* and *A. presbyter* (Table 3.3). It was the only time when *P. flesus* was recorded and these were at the post-larval stage (7-11 mm) (Figure 3.1 and Table 3.3). Secondly, between July and September, the species richness declined and there was a high relative abundance of *D. labrax*, *P. microps* and *A. presbyter* (Figure 3.1 and Table 3.3). The

'October - January' group was characterised by the presence of *Liza aurata* and *Liza ramada* which dominated the catch between November 2006 and January 2007 (Figure 3.2 and Table 3.3). The three species that had been dominant in summer, declined in abundance (Table 3.3).

The ordination analysis separated the monthly samples on the first axis into two main groups (Figure 3.3). The October - January group on the right was dominated by *L. aurata* and *L. ramada*, and the other samples which contained high numbers of *P. microps* were on the left. This second group was separated on Axis 2 into the February - April group and the May - September group which contained *D. labrax* and *A. presbyter*, which were absent from February to April.

For most species, especially *P. microps*, the periods of high abundance were also reflected in the biomass data (Table 3.4). Two exceptions were *D. labrax* and *A. presbyter* which had a relatively greater biomass due to the presence of small numbers of larger older juveniles in May to July, and May and June respectively (Table 3.4 and Figure 3.1).

Environmental conditions

The environmental conditions measured by the Environment Agency are presented in Figures 2.6 and 2.7. During the two fish sampling campaigns, the water temperatures ranged from 3.3 to 21.0 °C with minima occurring in January and maxima in August. The salinity ranged from 29.3 to 35.3, with minima occurring during periods of highest rainfall in winter. The pH remained stable throughout the sampling period. Spring peaks in dissolved oxygen concentrations, high chlorophyll concentrations and low transparency (turbidity), were consistent with the occurrence of an annual algal spring bloom in 2004, 2005, 2006.

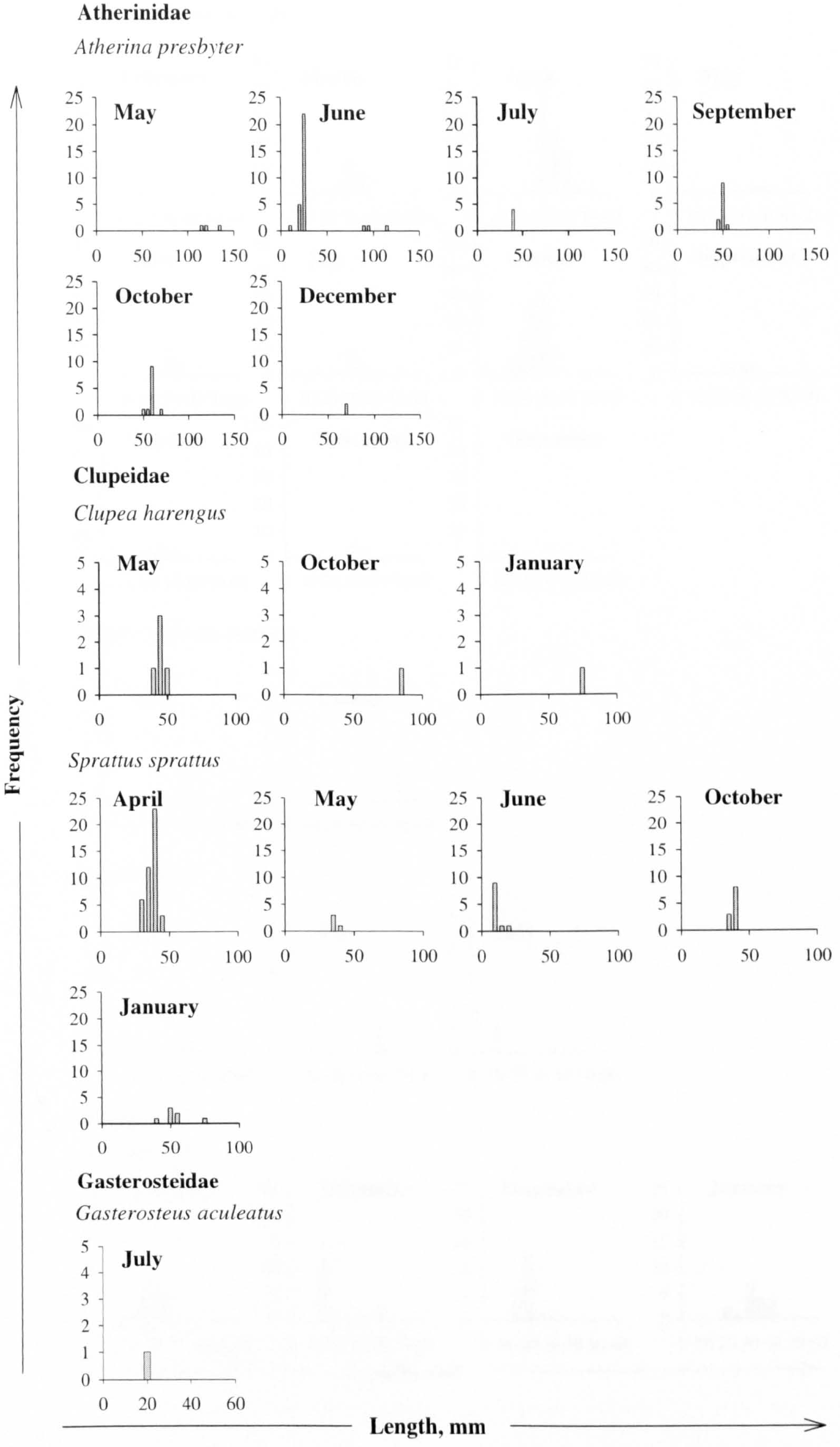
Quantitative catch (July and August 2007)

During July and August 2007, 10,037 fishes were collected from 10 species and seven families (Table 3.5). The mean abundance was 558 0.1 ha^{-1}, and the range was 76 to 2699 0.1 ha^{-1} $\pm$ 574 SD. There were no significant differences between the three sites, in the fish abundance or biomass, in July ($F = 0.2$ and 1.19 respectively, $P > 0.05$) or in August ($F = 0.6$ and 1.32 respectively, $P > 0.05$). In some instances the abundance changed by an order of magnitude within two days (Table 3.5). The catches were dominated by *D. labrax* between the 3^rd^ and 14^th^ July; and by *P. microps* between the 15^th^ July and 16^th^ August (Table 3.5). Although *A. minuta* was present but rare in the semi-quantitative survey in summer 2006, it was not recorded in 2007. Species not recorded in the semi-quantitative survey in summer 2006, but collected in 2007 in low abundances were: *L. ramada*, *L. aurata*, *S. sprattus*, *C. harengus*, *P. minutus*, *G. aculeatus*, and *S. aurata*. *S. aurata* was recorded for the first time on the east coast of the UK. The majority of fishes collected were a mixture of 0-group, 1-group or small adults, except in July when one large *L. aurata* individual (500 mm) was collected at Tollesbury, contributing disproportionately to the total biomass for the species.

Table 3.2: Relative numeric abundance and biomass, frequency of occurrence, mean fork length (mm $\pm$ 1 SD) and range of fork lengths, mm of fishes collected between February 2006 and January 2007 in the Blackwater estuary saltmarshes. The species in each guild were listed alphabetically according to family. Catch per unit effort: three 30-minute tidally- strained nettings each month

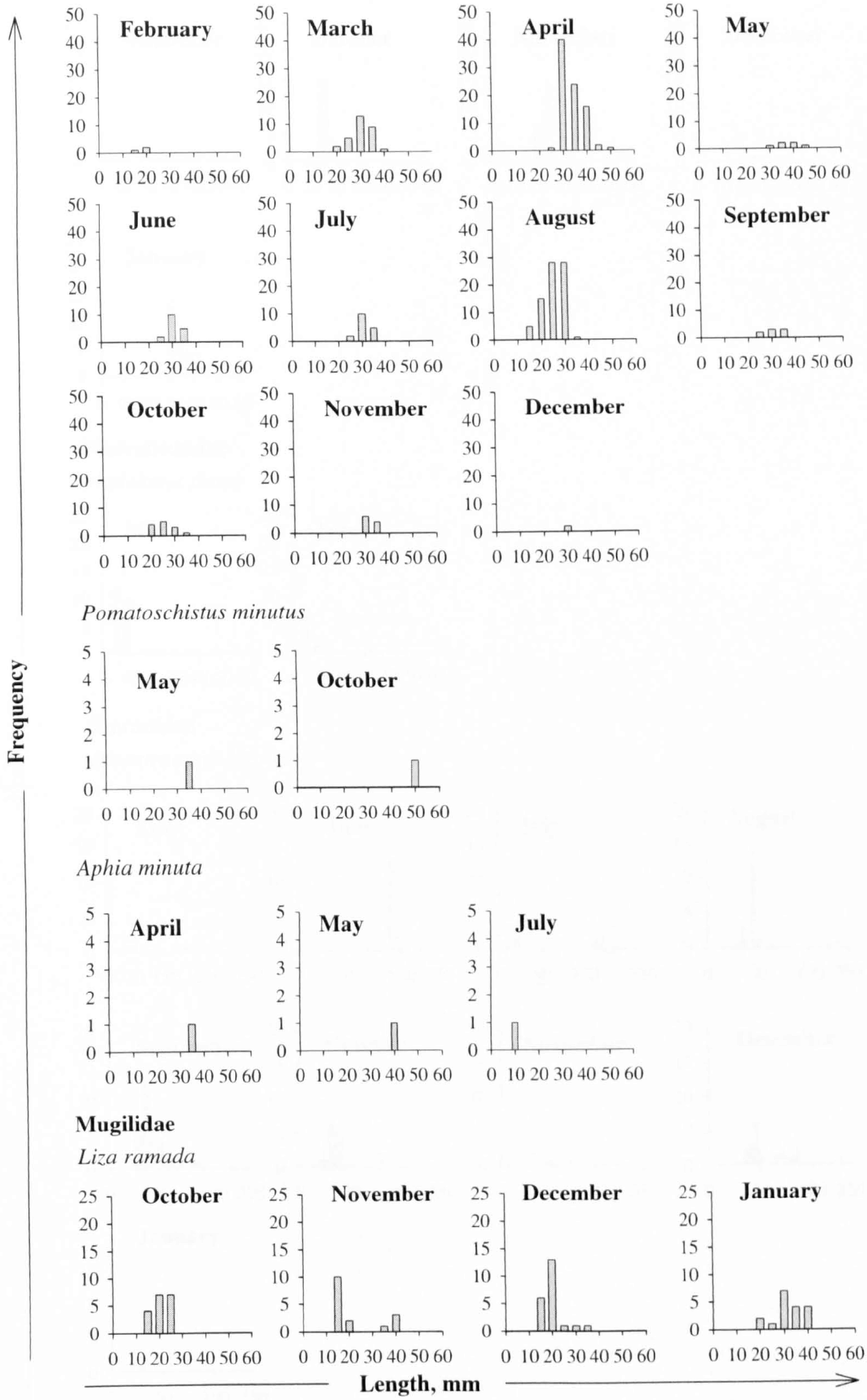
Ecological guild	Family	Species	% N	% B	%FO	Length, mm			
						Mean	±	SD	Range
Marine straggler			**10.1**	**2.2**	**25.0**				
	Clupeidae	*Sprattus sprattus*	10.0	2.2	41.7	36.2	±	11.3	10-55
	Syngnathidae	*Entelurus aequoreus*	0.1	0.0	8.3	20.0			
Marine estuarine dependant			**39.4**	**85.2**	**47.9**				
	Atherinidae	*Atherina presbyter*	8.4	10.6	50.0	46.7	±	27.4	10-136
	Clupeidae	*Clupea harengus*	0.9	1.1	25.0	58.0	±	58.0	42-89
	Mugilidae	*Liza aurata*	10.8	1.3	41.7	27.3	±	27.3	15-45
	Serranidae	*Dicentrarchus labrax*	19.3	72.3	75.0	54.1	±	31.4	18-230
Estuarine resident			**41.0**	**11.3**	**35.0**				
	Gobiidae	*Aphia minuta*	0.4	0.2	25.0	30.3	±	16.5	12-44
		Pomatoschistus microps	35.7	10.8	91.7	29.8	±	6.5	15-50
		Pomatoschistus minutus	0.3	0.2	16.7	42.5	±	10.6	35-50
	Pleuronectidae	*Platichthys flesus*	3.9	0.0	16.7	8.7	±	2.0	7-11
	Sygnathidae	*Syngnathus acus*	0.7	0.1	25.0	65.8	±	25.0	30-85
Diadromous			**9.5**	**1.4**	**20.8**				
	Gasterosteidae	*Gasterosteus aculeatus*	0.1	0.0	8.3	21.0			
	Mugilidae	*Liza ramada*	9.3	1.3	33.3	25.4	±	7.6	15-41

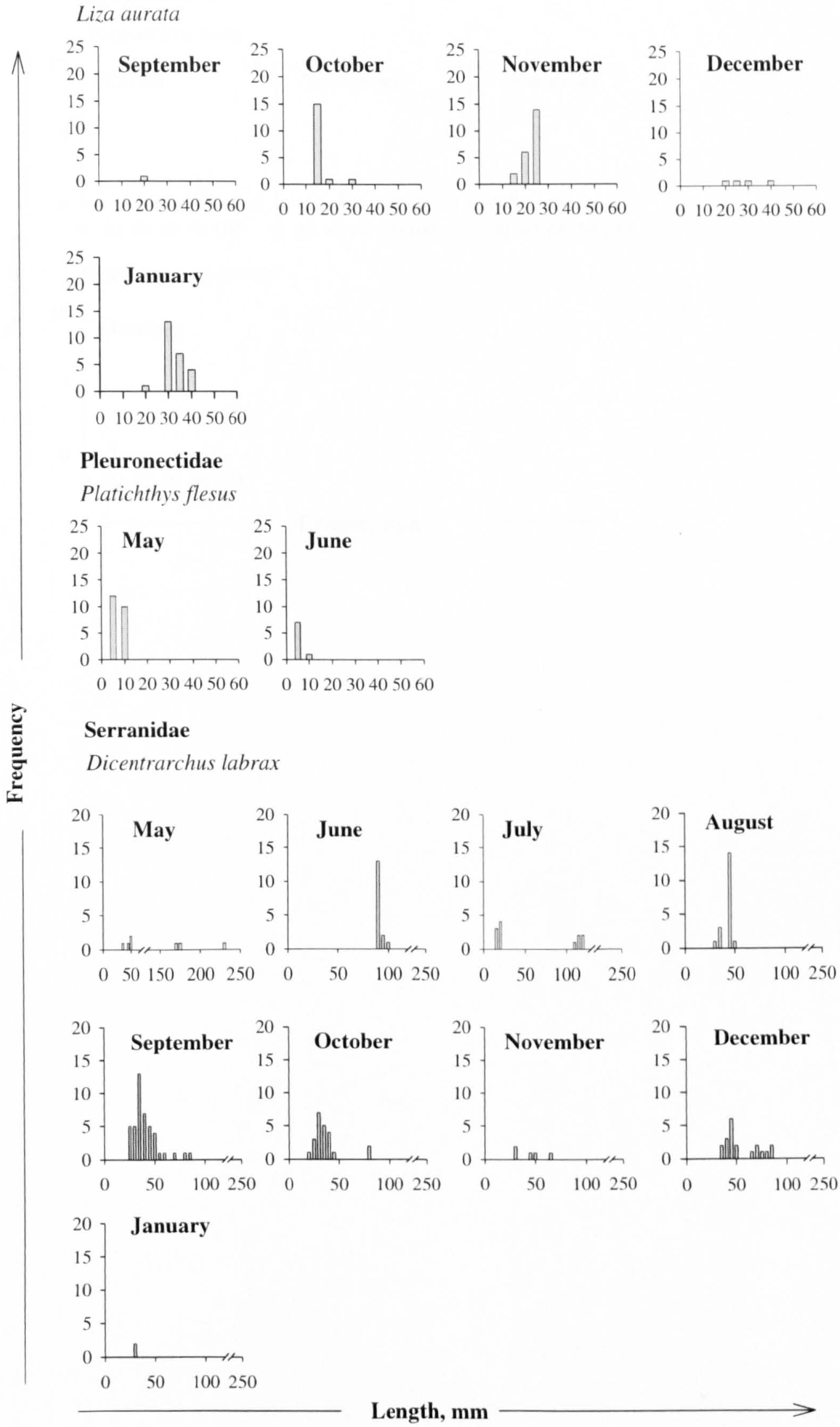
Figure 3.1: The length frequencies of fishes from the saltmarshes (Feb. 2006 –Jan. 2007)



Gobiidae

Pomatoschistus microps





Liza aurata
September
October
November
December
January
Pleuronectidae
Platichthys flesus
May
June
Serranidae
Dicentrarchus labrax
May
June
July
August
September
October
November
December
January
Frequency
Length, mm

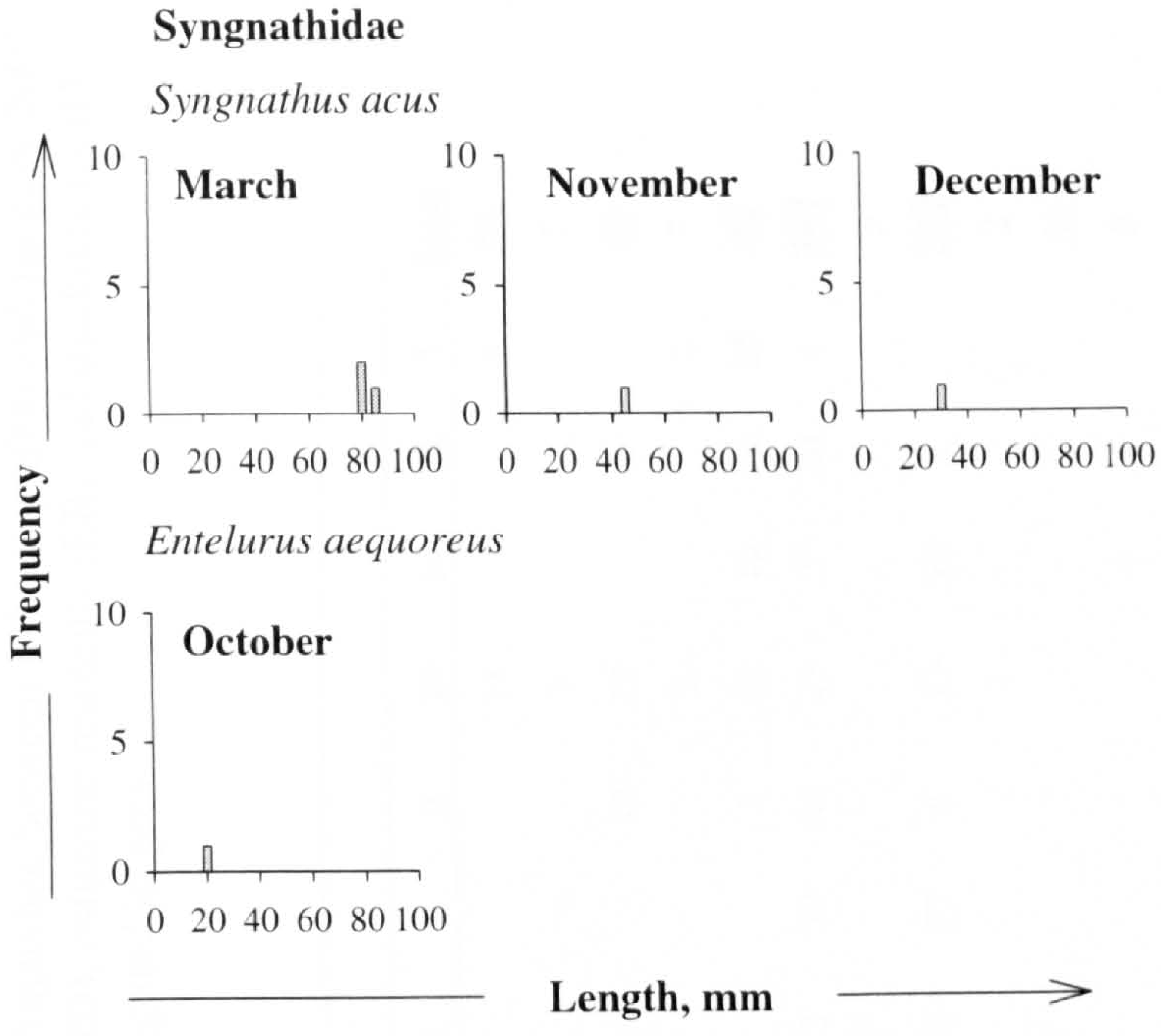

Syngnathidae
Syngnathus acus
March
November
December
Entelurus aequoreus
October
Frequency
Length, mm
0
5
10
0 20 40 60 80 100

Table 3.3: The numbers of fishes collected during each month in the Blackwater saltmarshes between February 2006 and January 2007. The ecological guilds (EG) are marine stragglers (MS), marine estuarine dependants (MD), estuarine residents (ER) and diadromous (DA). The abundances of the top six species, contributing 94% to the total abundance, are highlighted in grey

			Month												
EG	**Family**	**Species**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**1**	**Sum**
MS	Clupeidae	*Sprattus sprattus*			44	4	11				11			6	**76**
	Syngnathidae	*Entelurus aequoreus*									1				**1**
MD	Atherinidae	*Atherina presbyter*				3	31	4		12	12		2		**64**
	Clupeidae	*Clupea harengus*				5					1			1	**7**
	Mugilidae	*Liza aurata*								1	18	16	22	25	**82**
	Serranidae	*Dicentrarchus labrax*				7	16	12	19	44	23	5	20	1	**147**
ER	Gobiidae	*Aphia minuta*			1	1		1							**3**
	Gobiidae	*Pomatoschistus microps*	3	30	84	6	17	22	77	8	13	10	2		**272**
	Gobiidae	*Pomatoschistus minutus*				1					1				**2**
	Pleuronectidae	*Platichthys flesus*				22	8								**30**
	Sygnathidae	*Syngnathus acus*			3							1	1		**5**
DA	Gasterosteidae	*Gasterosteus aculeatus*					1								**1**
	Mugilidae	*Liza ramada*									17	32	4	18	**71**
Sum			**3**	**30**	**132**	**49**	**84**	**39**	**96**	**65**	**97**	**64**	**51**	**51**	**761**

Figure 3.2: Cluster analysis (Ward's method, Euclidean distances) on the log (x+1) transformed monthly densities of species collected between February 2006 and January 2007

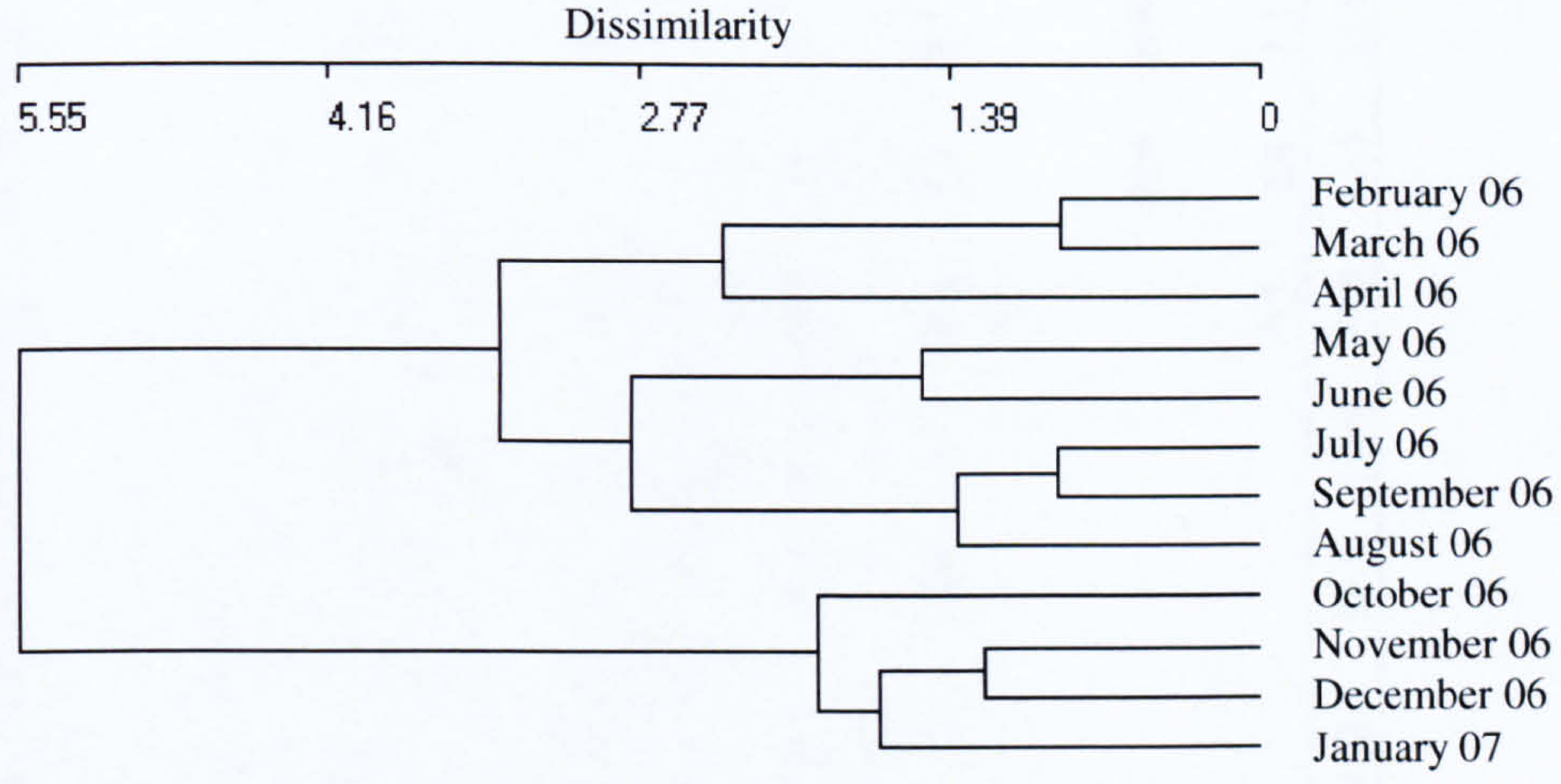


Figure 3.3: Covariance Principal Components Analysis on the log (x + 1) transformed monthly densities collected between February 2006 and January 2007. Species are shown in vectors. Only the vectors of the six main species (those with more than eight individuals in total) are illustrated for clarity. The squares represent the temporal clusters identified in the previous cluster analysis: February -April (red), May - September (green), October – January (yellow)

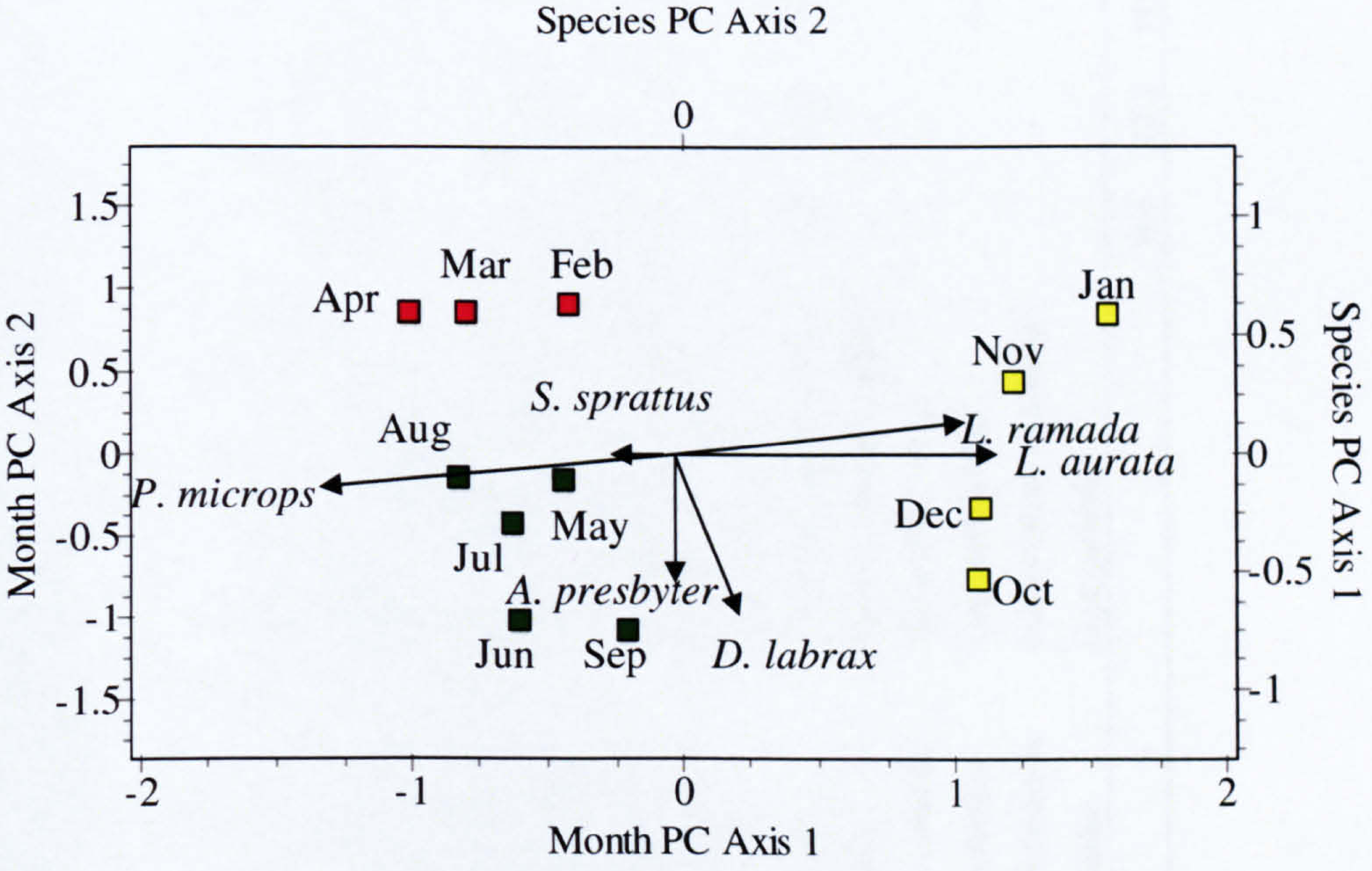


Table 3.4: The total biomass (grams) of the fishes collected during each month in the Blackwater saltmarshes between February 2006 and January 2007. The ecological guilds (EG) are marine stragglers (MS), marine estuarine dependants (MD), estuarine residents (ER) and diadromous (DA)

			Month											
EG	**Family**	**Species**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**1**	**Sum**
MS	Clupeidae	*Sprattus sprattus*			12.4	1.0	0.1				3.3			4.0	20.7
	Syngnathidae	*Entelurus aequoreus*									0				0
MD	Atherinidae	*Atherina presbyter*				42.8	25.0	1.6		9.7	17.5		4.8		101.5
	Clupeidae	*Clupea harengus*				2.5					4.9			3.1	10.5
	Mugilidae	*Liza aurata*								0.1	1.6	2.6	1.9	6.0	12.2
	Serranidae	*Dicentrarchus labrax*				316.7	145.8	98.4	16.2	43.5	19.9	5.9	47.3	0.3	694.0
ER	Gobiidae	*Aphia minuta*			0.6	0.9		0.01							1.5
	Gobiidae	*Pomatoschistus microps*	0.3	12.1	46.8	4.5	7.0	2.3	18.6	3.3	3.2	4.5	0.7		103.2
	Gobiidae	*Pomatoschistus minutus*				0.6					1.7				2.3
	Pleuronectidae	*Platichthys flesus*				0.2	0.1								0.3
	Sygnathidae	*Syngnathus acus*			1.0							0.04	0.01		1.1
DA	Gasterosteidae	*Gasterosteus aculeatus*					0.2								0.2
	Mugilidae	*Liza ramada*									0.7	2.4	1.1	8.5	12.8
Sum			0.3	12.1	60.8	369.2	178.0	102.3	34.8	56.6	52.8	15.5	55.8	21.9	960.0

Table 3.5: Density (fish abundance 0.1 ha^{-1}) (top) and biomass (grams 0.1 ha^{-1}) (bottom) of fishes (July and August 2007)

	Tollesbury			Orplands			Abbotts Hall			Abbotts Hall			Orplands			Tollesbury			Sum
	July									August									
Numbers 0.1 ha^{-1}	3	4	5	12	3	14	15	16	17	1	2	3	4	5	6	15	16	17	
Sprattus sprattus		1												7	2		1		**11**
Sparus aurata					1									4	4				**9**
Atherina presbyter	16	4	4	7	24	3	49	10		18	5	5	90	18	15	170	7	15	**460**
Clupea harengus	12		35											1					**48**
Liza aurata	18				11												1		**30**
Dicentrarchus labrax	311	64	149	633	345	118	209	132	64	200	50	39	139	187	86	951	254	259	**4190**
Pomatoschistus microps	29	6	35	17	5	3	513	273	96	428	400	204	569	280	310	1563	306	203	**5240**
Pomatoschistus minutus								2		8	9	2							**21**
Gasterosteus aculeatus		1									1			1		4			**7**
Liza ramada	10															11			**21**
Numbers 0.1 ha^{-1}	**396**	**76**	**223**	**657**	**386**	**124**	**771**	**417**	**160**	**654**	**465**	**250**	**798**	**498**	**417**	**2699**	**569**	**477**	**10037**
Biomass g 0.1 ha^{-1}																			
Sprattus sprattus		1												2	1		0		**4**
Sparus aurata					6									56	62				**124**
Atherina presbyter	43	23	24	0	4	12	19	3		14	4	2	51	13	19	84	7	13	**335**
Clupea harengus	21		71											3					**95**
Liza aurata	1627				68												0		**1695**
Dicentrarchus labrax	81	14	32	90	4544	145	108	68	18	119	30	28	95	154	84	691	199	223	**6723**
Pomatoschistus microps	11	2	14	4	3	1	249	128	45	229	238	98	270	110	134	710	148	96	**2490**
Pomatoschistus minutus								1		10	11	2							**24**
Gasterosteus aculeatus		0									0			13		1			**14**
Liza ramada	20															2			**22**
Biomass g 0.1 ha^{-1}	**1803**	**40**	**141**	**94**	**4625**	**158**	**376**	**200**	**63**	**372**	**283**	**130**	**416**	**351**	**299**	**1487**	**354**	**333**	**11525**

Discussion

Community composition

At least 72 species of fish have been recorded in the Blackwater Estuary (data provided courtesy of K. Markham, Environment Agency 2007), including *Sparus aurata* and *Liza aurata* which were first recorded in the current study. Fourteen fish species were collected within the saltmarshes of the Blackwater estuary during the current study, and of these, six species represented 94 % of the catch. The dominance of the community by a small number of fish species is common in the saltmarshes in Western Europe (Drake and Arias 1991a; Cattrijsse et al. 1994; Laffaille et al. 1998; Lefeuvre et al. 2000; Laffaille et al. 2001c; Salgado et al. 2004a; Salgado et al. 2004b), and elsewhere (Weinstein and Brooks 1983; Hettler 1989; Jin et al. 2007).

The estuarine resident *P. microps* was numerically dominant (36 % over the 12 months and 52 % in July and August 2007) and juvenile *D. labrax* dominated the biomass (72 % over 12 months and 58 % between July and August 2007). This finding is consistent with previous studies which show that the fish assemblages of western European saltmarshes are often dominated by estuarine resident species such as those belonging to the Gobiidae family, as well as marine juvenile species such as *D. labrax* (Drake and Arias 1991a; Mathieson et al. 2000; Hampel and Cattrijsse 2004).

Of the 21 species collected subtidally in 2006, nine were also collected in the saltmarshes. In addition, four species were present in the marshes but not recorded subtidally, including *S. aurata*, a species not recorded on the east coast of the UK before (S. Colclough, personal communication). To date, standard CEFAS and Environment Agency subtidal surveys do not routinely involve the examination of the pattern of melanophores or counting of the pyloric caeci in 0-group fishes. Therefore the lack of 0-

group golden and thin-lipped mullet in the subtidal surveys may be due to the misidentification of these species. The length-frequency histograms showed dominance by the smaller post-larval and juvenile 0-group fishes in the saltmarshes. Some 1-group fishes were also caught but larger fish were rare. This is in contrast to the large individuals that dominated the subtidal samples. Although the mesh size used subtidally was slightly larger (5 mm) than that used intertidally (2 mm) and may have targeted slightly larger individuals, previous authors have shown that 0-group fishes do use the shallow saltmarshes preferentially and larger individuals prefer the deeper subtidal habitats (Laffaille et al. 2000; Paterson and Whitfield 2000).

In species where no ontogenetic dietary shift occurs, the spatial and temporal differences in resource use minimise intraspecific competition (Cabral et al. 2002). However, most fishes present in the saltmarshes did exhibit an ontogenetic shift (Ferrari and Chieregato 1981 and see Chapter 5). Therefore in general, the 0-group preference for saltmarshes is more likely to be a balanced response to the expanding foraging opportunities and the reduced predation risk in shallow water, but carries the risk of being stranded on the ebb tide (Kneib and Wagner 1994; Franco et al. 2006).

Temporal variations

The fish assemblage of the Blackwater saltmarsh was characterised by three groups: February-April, May-September, and October–January. This trend is consistent with other European and North American saltmarshes where the abundance varies predictably according to the timing of spawning and recruitment (Bozeman and Dean 1980; Whitfield 2004; Mees et al. 2005; Ramos et al. 2006). In this study, no clear relationship was found between the fluctuating environmental conditions within the saltmarshes and the (predominantly 0-group) fish community structure.

Three gravid *A. presbyter* were collected in May, indicting that this is their spawning period, as it is in the Mediterranean (Moreno et al. 2005). 0-group individuals first appeared in June, and were present until December. None was collected between February and April (Figure 3.1). This 'marine estuarine dependant' species reaches the northern limits of its distribution within British waters (Palmer and Culley 2006).

The first record for the 'marine straggler' *Sparus aurata* in Eastern England, nine 1-group fish, may be a consequence of the northern extension of its range in summer due to increasing sea surface temperatures (Cabral et al. 2001; Fahy et al. 2004; Craig et al. 2008).

0-group *Liza ramada* and *Liza aurata* first appeared in the saltmarshes in October. *L. ramada* spawns in early autumn in Britain and 0-group individuals 18-24 mm long were found in the Thames Estuary between September and November (Colclough et al. 2002; Davies et al. 2004). The exact time of spawning of *L. aurata* is not known although it is likely to be similar to *L. ramada* (Reay and Cornell 1988). The pattern of autumn spawning is in contrast to the Mont Saint-Michel Bay (Northern France) where *L. ramada* use the saltmarshes between March and November, and not in the colder winter months (Laffaille et al. 2002). It is likely that *L. ramada*, mainly enter the saltmarshes during their migration inshore (Laffaille et al. 2000).

The 'estuarine resident' *P. microps* was recorded in the saltmarshes between February and December 2006 and the smallest individuals (15 mm) appeared in February. In the Westerschelde Estuary *P. microps* is present between June and October (Cattrijsse et al. 1994) and in the Thames Estuary, the smallest *P. microps* appear in June (Colclough et al. 2002). *P. microps* is a euryhaline and eurythermal species, tolerant of a wide range of environmental conditions (Dolbeth et al. 2007) and spawns over a relatively long period from March to September (Pampoulie 2001). *P. microps* was more abundant in the saltmarshes than *P. minutus* whereas subtidally *P. minutus* was more abundant than *P. microps*. This spatial segregation is consistent with a Swedish study which showed that when these two species coexist, *P. microps* migrates to the vegetated intertidal habitats (Magnhagen and Wiederholm 1982).

Post-larval *P. flesus* (7-11 mm) were collected only in the saltmarshes and only in May and June (Table 3.3). In early May, postlarval *P. flesus* > 7 mm also appear in multiple waves in the Thames Estuary (Colclough et al. 2002). *P. flesus* is a facultatively catadromous species which migrates to the sea to spawn between February and June (Wheeler 1969). The exact spawning time is variable: the migration from the estuary to spawn has occurred two months earlier in years when water temperatures were up to 2 °C colder, during which times the arrival to the spawning ground was also more synchronised (Sims et al. 2004). The euryhaline postlarvae then migrate upriver into the freshwater reaches in late spring. This explains why there was an absence of flounder in the saltmarshes by July.

During the present study, twenty 0-group bass were collected in December when the average temperature was 6 °C and only one bass was collected in January 2007 when the average temperature was 4 °C. Previous writers have shown that 0-group bass are unable to survive below 6 °C (Kennedy and Fitzmaurice 1972; Kelley 1988a; Lancaster 1991) and migrate to adjacent warmer, deeper, subtidal habitats when the water temperature begins to decline from October onwards (Claridge and Potter 1983; Aprahamian and Barr 1985; Kelley 1986; Laffaille et al. 2000a). These migratory patterns are not seen in bass caught in warmer waters and are a local adaptation to cold winters (Pawson et al. 2000). Young bass are faithful to their natal estuaries for the first four or five years of their lives (Pickett and Pawson 1994). The presence of 1 to 2-group bass in the Blackwater saltmarshes in July 2007 shows that the 2005 and 2006 cohorts survived locally, despite the decommissioning of Bradwell nuclear power station in 2002, and this may be indicative of a general northwards migration resulting from increasing water temperatures (Turnpenny 1988; Pawson et al. 2005; Joyce 2006).

0-group *D. labrax* were abundant in the saltmarshes between summer and autumn (7.6 - 20 °C) (Figures 3.1 and 2.6) after being spawned between February (offshore) and May (inshore) in water temperatures between 9.5 and 11 °C (Sabriye 1986; Henderson and Corps 1997; Pawson and Eaton 1999; Pawson et al. 2000). The length-frequency data (Figure 3.1) show that small numbers of 0-group bass first arrived in May. These individuals were probably spawned offshore in February. A second group of smaller 0-group bass then arrived in the saltmarshes in July, probably having been spawned inshore later in the spring, as occurs in other UK sites such as in the Severn Estuary (Aprahamian and Barr 1985; Pickett and Pawson 1994). The growth rates of the second (inshore) 0-group cohort show that bass grow the most during summer (July to September), when they are most abundant in the saltmarshes, a finding which is consistent with Kelley (1988b).

Abundance estimates

This study is the first on the Blackwater Estuary to quantify the mean abundance of fishes using saltmarshes in the Blackwater Estuary (558 0.1 ha^{-1}). The high range between samples (76 - 2699 0.1 ha^{-1} $\pm$ 574 SD) illustrates the variable nature of these habitats (Colclough et al. 2005). The fact that the quantitative catch was always highest on the first day of sampling is unexpected. It might indicate that the first catch depleted the local populations but these habitats are part of an open system. However, it is possible that there are locally faithful shoals of fishes which were being progressively depleted. In the US, although the home range of large 0-group *Fundulus hereroclitus* at high tide was reported to be 15 ha, at low tide the fishes exhibited a strong site fidelity to a particular created creek (Teo and Able 2003). This is important because it would suggest that the loss of an area of intertidal foreshore may have significant consequences for a local fish population as local stocks are displaced. One way to measure this movement may be through the use of stable isotope ratio analysis (Gillanders et al. 2003).

The abundance and biomass of the fishes collected from the three sites during summer 2007 were not significantly different, despite the fact that only Abbotts Hall and Tollesbury managed realignment sites are surrounded by saltmarsh. Thus the presence of natural saltmarsh may not be essential for fish use of managed realignment sites.

Nursery habitats

Elliott and Hemmingway (2002) define a fish nursery as simply a concentration of juvenile stages which are feeding and growing. However, Beck et al. (2001) provide a more strict nursery habitat definition, as an area which contributes more per unit area on average to the production of individuals that recruit to the adult population, than the production from other habitats in which juveniles occur. To provide evidence that these habitats are nursery grounds using the second, more detailed definition, further research is required to quantitatively compare intertidal and subtidal habitats on all temporal scales with respect to the 0-group feeding, densities, survival rates, and the specific contribution of juveniles to the adult stock.

Many US writers have commented on the importance of vegetated marsh surfaces for fishes (Weisberg et al. 1981; Boesch and Turner 1984; Rozas et al. 1988; Peterson and Turner 1994; Thomas and Connolly 2001). US marshes are dominated by smooth cord grass *Spartina alterniflora* which provides refuge, and potential spawning sites (Kneib 1986). The fishes exhibit preferences for the vegetated marsh surfaces by moving into them actively on the flooding tide (Hettler 1989; Minello and Zimmerman 1992; Kneib and Wagner 1994). For example, Weisberg et al (1981) showed that although the feeding activity was greatest during high tides regardless of marsh inundation, killifish *Fundulus hereroclitus* enter the vegetation whenever possible.

However, the structure of European vegetated marsh surfaces is different from US marshes and in this study the sites were dominated by non-shrubby pioneer annual succulent halophytes which proliferate in summer and die-back during late autumn. In European saltmarshes the vegetated surfaces cannot be used by fishes for refuge as much as the US marshes because of the large tidal ranges and it is argued that the main refuge benefits of saltmarshes are due more to the shallowness of the habitats and the high turbidities in the creeks (Cattrijsse et al. 1994; Hampel et al. 2003). It is likely that the most effective preservation of estuarine fish diversity will involve the conservation of both complex vegetated and less complex unvegetated habitats (Guidetti 2000). The type of optimal vegetation may vary between estuaries for the same species (Goldberg et al. 2002). One aspect not yet fully recognised in European saltmarshes is the value of vegetated habitats in providing access to an increased surface area for potential invertebrate food sources (McIvor and Odum 1988; Madon et al. 2001). In European saltmarshes these sources may include shredding amphipods and detritivorous shore crabs (Laffaille et al. 2001b). Therefore to fully appreciate the value of the vegetation to the fishes, the site specific benefits from these food sources must first be ascertained.

Chapter 4: Utilisation of coastal managed realignment areas and saltmarshes in SE England by juvenile bass *Dicentrarchus labrax* (L.)

Introduction

Feeding by fish is an important function of natural and created intertidal habitats (Weisberg et al. 1981; Rozas and LaSalle 1990; Cattrijsse et al. 1994; Nemerson and Able 2003). The knowledge of fish feeding behaviour may be used for improved design and management of future managed realignment schemes. Little work has been published within the UK of the value of ancient eroding saltmarshes and created habitats in managed realignment areas for fish feeding.

Aim

The aim of this study was to quantitatively assess the feeding ecology of 0-group *Dicentrarchus labrax* (L.) (in their first year of life, less than approximately 90 mm) in three managed realignment sites in SE England, that have developed into different habitats, and two ancient saltmarshes. As seasonal variation plays a large role in fish feeding behaviour (Colclough et al. 2005) the differences in diet between summer and autumn were also examined. Three hypotheses were tested:

a) the restored and established saltmarshes in SE England are of equal feeding value to 0-group bass when they are accessed on high spring tides;

b) the composition of small and large 0-group bass diets will vary between the sites because of differences in the time available to feed and the microhabitat structure;

c) the composition of large 0-group bass diets will vary between summer and autumn

Bass was chosen because of its abundance in UK saltmarshes (Pickett and Pawson 1994) and because a limited amount of research had already been conducted on this species in these habitats (Colclough et al. 2005). The feeding ecology of 0-group bass has been investigated in natural saltmarshes in the Gulf of Lion and Mont-Saint Michel Bay, France (Roblin and Brusle 1984; Laffaille et al. 2001b), the Upper Scheldt Estuary, Belgium (Maes et al. 2003), the Tagus Estuary, Portugal (Cabral and Costa 2001), in fish ponds in Cadiz, Spain (Arias 1980), the Po River delta, Italy (Ferrari and Chieregato 1981) and in the Severn Estuary and South Wales coast in the UK (Aprahamian and Barr 1985; Lancaster 1991). No 0-group bass feeding ecology studies have been conducted in natural marshes or in restored habitats within MR sites in S.E. England.

Methods

Field sites

Bass were collected from Tollesbury, Orplands and Abbotts Hall realignment sites, and the ancient saltmarshes adjacent to the Tollesbury and Abbotts Hall realignment sites in the Blackwater Estuary, Essex, SE England (Figure 2.1). See Chapter 2 for site details.

Field methods

The fish were collected using a static funnel net with a mouth of 2 m square and 4 mm mesh (2 mm in the cod end) that was held across creeks on flooding and ebbing tides for 30 minutes, or until at least ten fish had been caught (see Chapter 2 for further fish collection details). Samples were collected every month between June and November when the bass are present; in 2005 and 2006; in daylight as bass are sight feeders; and on spring tides to ensure maximum fish use of each site. The fish were placed in ice immediately to slow the rate of digestion and were frozen within a few hours. Triplicate samples were collected with a zooplankton net (250 µm mesh) at the time of fishing. Prey availability was not assessed to quantify prey selectivity but site-specific invertebrate surveys have been carried out by other authors and the diets are discussed in this context.

Laboratory methods

In the laboratory, the length from the nose to the fork in the tail of each fish was measured and its digestive tract was removed. The contents of the oesophagus and stomach were removed for identification of the most recently consumed prey items (Berg 1979) and because in the intestine the food is often digested beyond recognition. The wet body weight (BW) of each fish without the gut contents, was recorded. Each prey item was identified to the lowest possible taxonomic level and its wet weight was recorded. The weights of the smaller prey items (e.g. copepods and larvae) were calculated as the mean of the weight of five to ten specimens. The proportion of fish that had empty stomachs was calculated to give the vacuity index (% V). The biomass of prey was chosen to determine the value of the prey to the fish, rather than measuring the frequency of prey occurrence, the prey abundance, or a combined index (Hyslop 1980), because of the large variations in the sizes of the prey and because the prey biomass is the best proxy for assessing the nutritional value of the prey.

Data analyses

The bass were allocated to 10 mm size classes, except the smallest class which included 15-19 mm fish since the smallest fish found was 15 mm long, and the class containing the largest fish which included 120-230 mm bass. Preliminary examination of the data showed there was a shift in the diets from zooplankton to more benthic prey at around 30 mm. Consequently two size classes were used for dietary analysis: 15-29 mm and 30-59 mm, hereafter referred to as 'small' and 'large' 0-group bass. Insufficient numbers of bass larger than 60 mm were caught for size-specific spatio-temporal analysis. By autumn, small bass were no longer present in sufficient numbers for gut contents analysis. In autumn insufficient numbers (<10) of bass were collected from the established saltmarsh adjacent to Abbotts Hall, therefore this site was not included in the dietary analysis. Thus the diets of three 'groups' of bass were used in the analysis of two comparisons: small and large bass from summer, and large bass from summer and autumn.

The feeding value of the five sites to bass was assessed by comparing the index of instantaneous ration (% IR), calculated as the total prey weight as a percentage of the fish weight, of bass entering and leaving each site. As the data were not normally distributed, the instantaneous ration within each group was compared statistically using the non-parametric Kruskal-Wallis test. As there were significant differences between the fullness of bass within the three groups ($P < 0.001$) pairwise comparisons within the three groups were conducted to compare site and tidal state, using the Mann-Whitney U test.

Principal Components Analysis (PCA) (Community Analysis Package 3.0 software © PISCES Conservation Ltd) was used to identify the similarities between the diets of small bass in summer and large bass in summer and autumn. A PCA matrix of replicates by groups was used to isolate a new set of variables and predict the structure in relationships between the original variables by maximising the amount of variation accounted for by the new axis (Clarke and Green 1988). The data were percentages, therefore a covariance, rather than standardising correlation, PCA matrix was used. This had the added benefit of reflecting differences in prey abundance, but can result in the dominant species determining the output. The percentage data were square root transformed to reduce the influence of abundant prey types.

One-way analysis of similarity (ANOSIM) was used to compare the differences between the average similarity of the individual bass diets, within and between the sites. ANOSIM was based on a Bray-Curtis rank similarity matrix, calculated using square root transformed data. The ANOSIM R-statistic is analogous to the f-test in ANOVA and was first calculated to determine whether significant differences existed between all groups. If the differences were significant ($P < 0.05$) then pair-wise comparisons between sample groups were conducted. Because of the large number of pairwise comparisons a Bonferroni correction was used to control the family-wise Type 1 error rate (the probability of accepting a false result) within small and large bass from summer (groups 1 and 2). When R equalled zero there were no differences between the sites and when R equalled one, the diets within a site were more similar to each other than the diets of bass within the other sites. Similarity percentage analysis (SIMPER) also based on the Bray-Curtis similarity measure, was used to determine the relative contributions of the discriminant prey types to the average similarity within sites, and to the dissimilarity among sites.

Results

Ontogenetic dietary shift

Of the 533 bass caught, 90 % were 0-group (less than 90 mm long). The bass diets changed with fish size (Figure 4.1). The smallest fish (15-19 mm) fed predominantly on calanoid copepods, with the remainder of the diet being planktonic larvae, and harpacticoid copepods. Increasingly larger fish took a greater proportion of progressively larger and benthic taxa (Figure 4.1). Generally, fish smaller than 30 mm had a narrow diet 'width', with 90 % of the prey coming from only six prey types, while larger fish had a greater diet width. Bass greater than 120 mm consumed only *Carcinus maenas*. On the basis of this difference in diets fish were divided into small (<30 mm) and large (30-59 mm) sizes for comparisons of the sites.

Spatio-temporal differences in instantaneous ration (IR)

Most small 0-group bass entering Orplands and Tollesbury realignment sites on the flood tide had empty guts (73 % and 69 %, respectively), while all those that entered the Abbotts Hall realignment site had been feeding immediately prior to capture (Table 4.1). Although the amounts of food in the guts of these fish were relatively small (Figure 4.2), they were significantly higher than those in the fish entering Orplands and Tollesbury (Table 4.2). No small bass caught on the ebb tide had empty guts and at all five sites there was significantly more food in the guts of the small bass caught on the ebb tide than on the flood tide (Figure 4.2, Tables 4.1 and 4.2).

Some of the large 0-group bass caught on the flood tide had empty guts, including the majority at Tollesbury in both summer (67 %) and autumn (61 %) (Table 4.1). In summer, large bass too had a significantly higher IR index on the ebbing tide than the flooding tide at the Tollesbury realignment site and the two saltmarshes, but not at

Abbotts Hall MR and Orplands MR. In autumn, the amounts of food in the guts of large fish leaving the Tollesbury and Orplands realignment sites and the Tollesbury saltmarsh were significantly greater than in those of fish caught on entering them (Tables 4.1 and 4.2, Figure 4.2). The amounts of food consumed by large bass were not significantly different in summer and autumn (Figure 4.2).

Figure 4.1: Proportion of prey types in ascending order of mean biomass, in the diets of bass from the Blackwater Estuary (summer-autumn 2005-06)

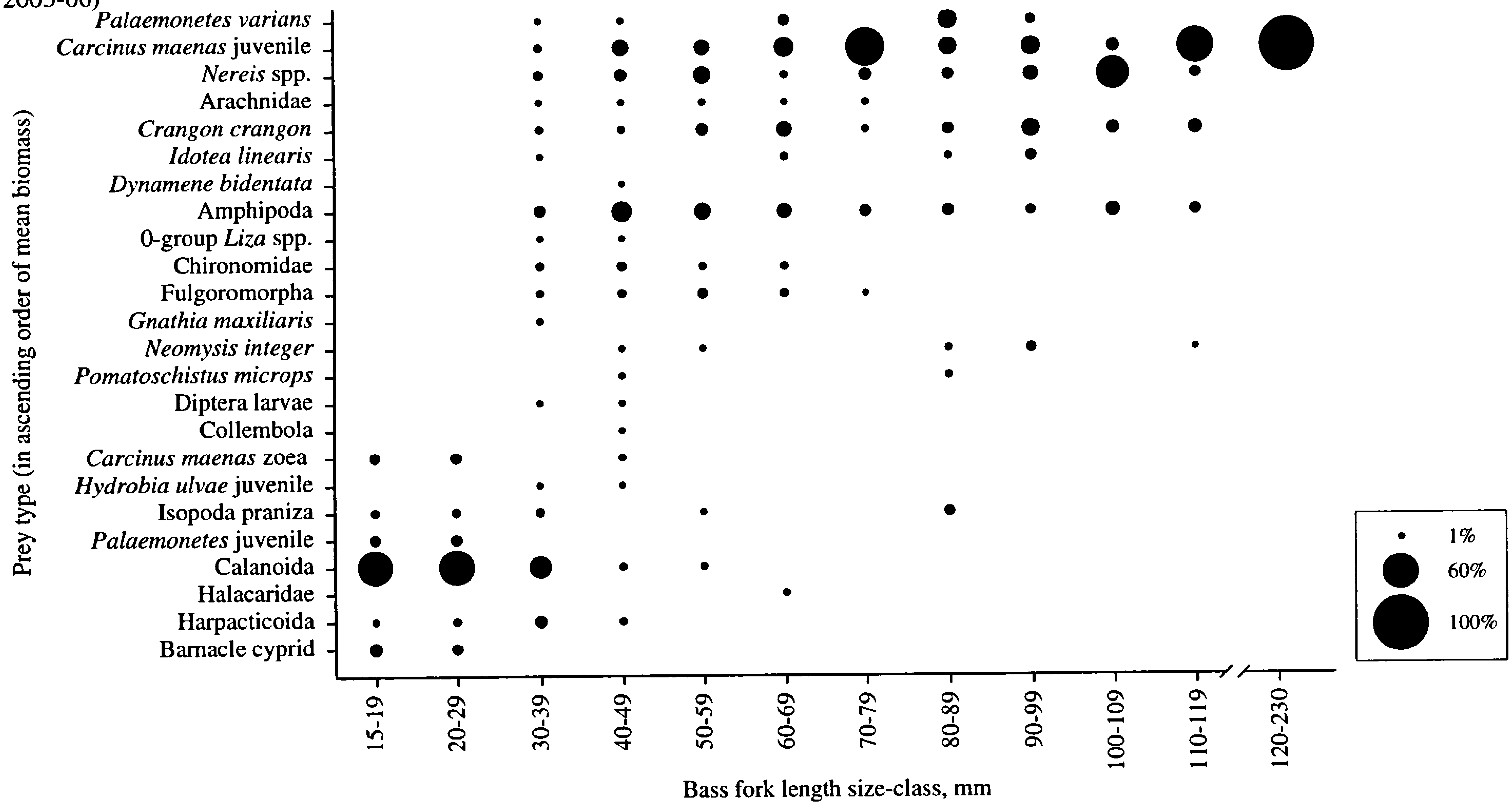


Table 4.1: The vacuity index (%V) (the mean percentage of bass with empty stomachs), of small (15-29mm), and large (30-59mm) 0-group bass caught on the flood and ebb from the three managed realignment sites, as well as established saltmarshes adjacent to Tollesbury and Abbotts Hall. The number, n, of bass sampled is given in brackets. MR = managed realignment, Established = adjacent established saltmarsh

Site		Tide	Small Summer		Large Summer		Large Autumn	
			%V	n	%V	n	%V	N
Tollesbury	-	Flood	69	(16)	67	(21)	61	(31)
	MR	Ebb	0	(10)	0	(16)	0	(58)
	Established	Ebb	0	(16)	0	(38)	0	(19)
Abbotts Hall	-	Flood	0	(20)	20	(15)	21	(14)
	MR	Ebb	0	(12)	0	(32)	6	(32)
	Established	Ebb	0	(21)	7	(28)		
Orplands	-	Flood	73	(15)	18	(40)	26	(27)
	MR	Ebb	0	(21)	0	(27)	6	(71)

Figure 4.2: The instantaneous ration of 0-group bass entering and leaving the sites (summer-autumn, 2005-06). Boxes, black and dotted lines are interquartile ranges, medians and means. Top and bottom whiskers and black circles are the largest and smallest non-outlier observations and 95th percentiles. MR = managed realignment, Established = adjacent established saltmarsh

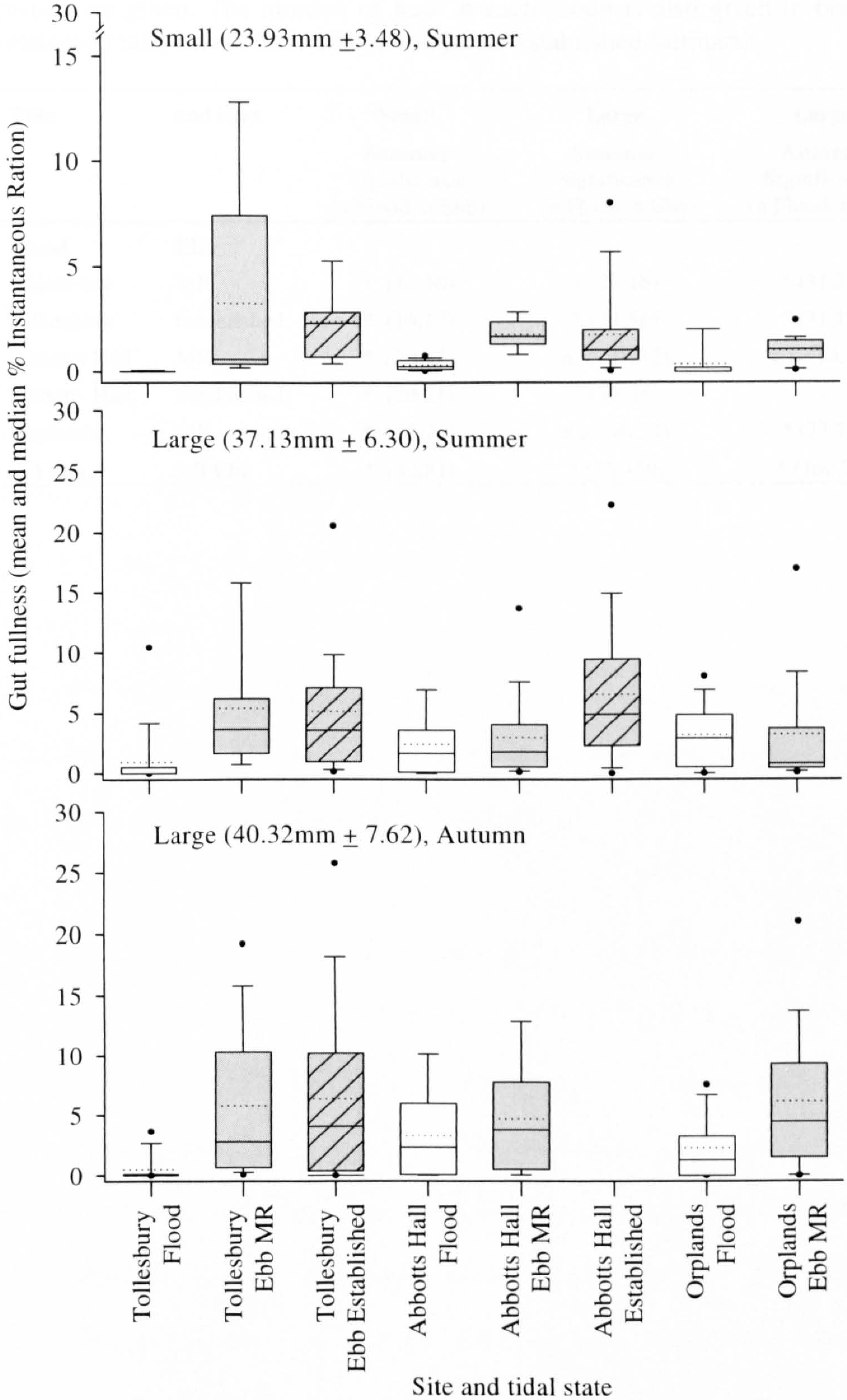


Table 4.2: Mann-Whitney U pairwise statistical comparisons of the median instantaneous ration, % IR, of small (summer) and large (summer and autumn) bass entering (Flood) and leaving (Ebb) the five sites. No significant differences were found between the instantaneous ration of bass leaving any sites on the ebbing tide, or between summer and autumn for large fish. Significant (*) ($P < 0.05$) and insignificant (n.s.) results are given. The number of bass in each group is also given in brackets. MR = managed realignment, Established = adjacent established saltmarsh

Tide	and sites	Small	Large	Large
		Summer Significance (n Flood, n Ebb)	**Summer** Significance (n Flood, n Ebb)	**Autumn** Significance (n Flood, n Ebb)
Flood	**Ebb**			
Tollesbury	MR	* (16,10)	* (21,18)	* (31,58)
Tollesbury	Established	* (16,17)	* (21,54)	* (31,19)
Abbotts Hall	MR	* (20,12)	n.s. (15,32)	n.s. (14,18)
Abbotts Hall	Established	* (20,21)	* (15,28)	-
Orplands	MR	* (16,21)	n.s. (40,27)	* (27,71)
All Flood	**All Ebb**	* (52,81)	* (76,159)	* (166,72)

Spatio-temporal differences in the diets

The diets of the small 0-group bass caught in summer from all five sites were dominated by planktonic crustaceans, particularly calanoid copepods which formed between 56 % and 84 % of the prey biomass consumed (Figure 4.3, and Tables 4.3 and 4.4). Harpacticoid copepods also contributed to the high (>50 %) similarities of the diets of fish within the Abbotts Hall realignment site and the Orplands realignment site, but not at the Tollesbury realignment, where more barnacle cyprids were consumed (Figures 4.3 and 4.4 and Table 4.4). The consumption of barnacle cyprids at Tollesbury was the reason for the significant difference in the average similarity of the diets of small bass in summer overall (ANOSIM, $R = 0.13$, $P < 0.05$) (Table 4.3). Only four prey taxa were consumed by small 0-group bass at the Abbotts Hall and Tollesbury realignment sites and Tollesbury saltmarsh (Figure 4.4). Seven taxa were eaten at Orplands and the Abbotts Hall saltmarsh, but barnacle cyprids, *G. maxilliaris*, *C. maenas* zoea, and *Hydrobia ulvae* constituted less than 4% of the mean biomass in these diets (Figure 4.3). The diets of small bass in summer from the managed realignments, were similar to those from the relic saltmarsh overall (Table 4.3).

The diets of large 0-group bass leaving the five sites in summer were significantly different overall (ANOSIM, $R = 0.14$, $P < 0.05$) (Figure 4.5). Over the five sites, calanoid copepods (22 %), *Carcinus maenas* (22 %), amphipods (20 %) *Crangon crangon* (10 %) and *Nereis* spp. (10 %) were important prey. Calanoid copepods were the most abundant prey type at the three realignment sites, but at all five sites the diets also contained larger and mostly benthic or demersal prey. This was particularly noticeable at Tollesbury MR and both saltmarsh sites, where fewer calanoid copepods were consumed and there was a high frequency of occurrence of small *C. maenas* (36-54 % compared to 13-15 % at Orplands and Abbotts Hall MR) (Figure 4.5).

In summer there were some significant differences between the diets of large 0-group bass between the sites (Table 4.3). However, there was also a large amount of within-site variation. The diets of the fish from the three managed realignment sites were similar to each other, but different to the two saltmarsh sites, where *C. maenas* (72 %) and amphipods (81 %) were more important contributors to the average similarity (Table 4.3). This trend was reflected in the overall significant difference between the diets of the large bass in summer from the managed realignments, and from the established saltmarsh (ANOSIM, $R = 0.2$, $P < 0.05$) (Table 4.3).

Figure 4.3: The proportion of prey types in ascending order of mean biomass, in the diets of small (15-29 mm) 0-group bass, collected from five sites in the Blackwater Estuary, in summer 2005-6 (number of bass = 83). MR = managed realignment, Established = adjacent established saltmarsh. The bubble size is proportional to the percentage of the prey type in the diet

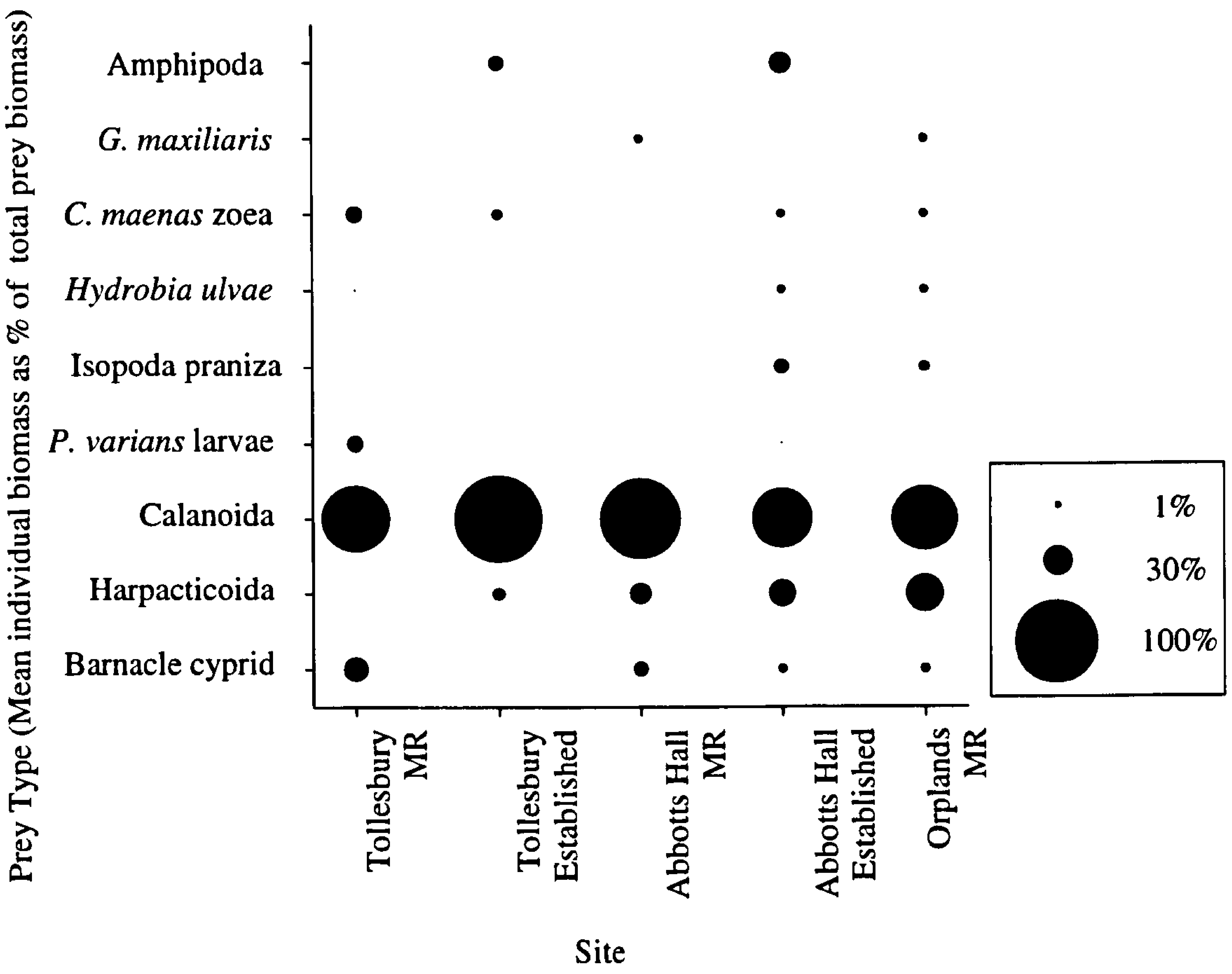


Figure 4.4: Covariance Principle Components (PC) Analysis of the diets of small bass (15-29 mm) in summer, leaving Abbotts Hall (red), established saltmarsh adjacent to Abbotts Hall (green), Tollesbury (blue), established saltmarsh adjacent to Tollesbury (grey) and Orplands (yellow) on the ebbing tide, in relation to prey type vectors (black arrows)

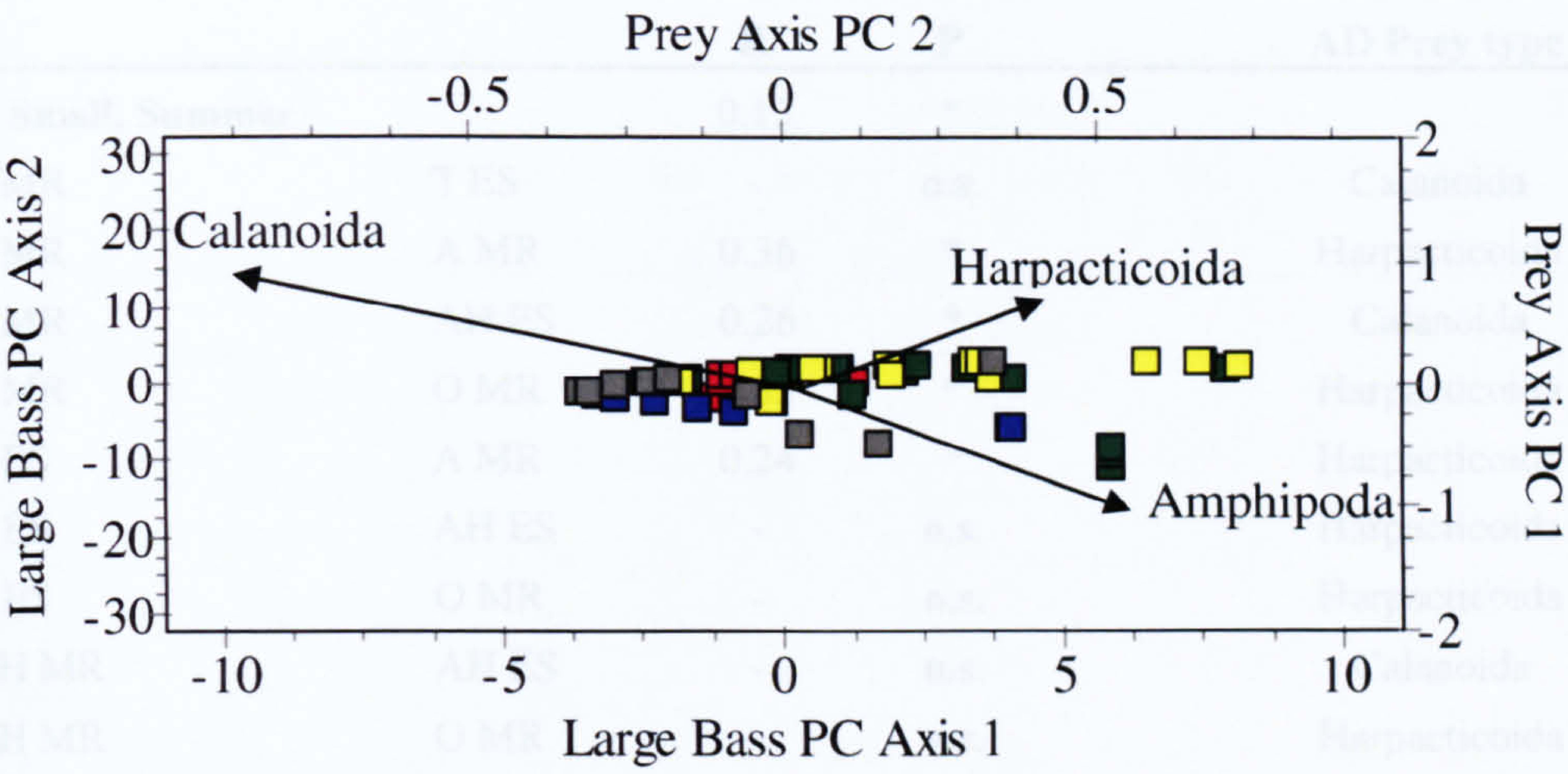


Table 4.3: ANOSIM (R and P value) and SIMPER (AD prey type = prey type contributing the most to the average dissimilarity, % Cont. = percentage contribution) for four groups of fishes from the Blackwater saltmarshes. T = Tollesbury, AH = Abbotts Hall, O = Orplands, MR = managed realignment, ES = established saltmarsh. Significant (*: P < 0.05 except for in groups 1 and 2 where P < 0.005) and insignificant (n.s.) results are given

Sites		ANOSIM		SIMPER	
		R	P	AD Prey type	% Cont.
1: Small, Summer		0.13	*		
T MR	T ES	-	n.s.	Calanoida	29.34
T MR	A MR	0.36	*	Harpacticoida	30.94
T MR	AH ES	0.26	*	Calanoida	24.01
T MR	O MR	0.33	*	Harpacticoida	32.99
T ES	A MR	0.24	*	Harpacticoida	39.83
T ES	AH ES	-	n.s.	Harpacticoida	29.02
T ES	O MR	-	n.s.	Harpacticoida	41.65
AH MR	AH ES	-	n.s.	Calanoida	25.5
AH MR	O MR	-	n.s.	Harpacticoida	37.83
AH ES	O MR	-	n.s.	Harpacticoida	29.96
MR	**ES**	-	n.s.	Calanoida	43.90
2: Large, Summer		0.14	*		
T MR	T ES	0.15	*	Amphipoda	27.52
T MR	AH MR	-	n.s.	Calanoida	24.19
T MR	AH ES	0.13	*	*C. maenas*	22.01
T MR	O MR	-	n.s.	Calanoida	20.6
T ES	AH MR	0.27	*	Amphipoda	27.26
T ES	AH ES	-	n.s.	Amphipoda	32.35
T ES	O MR	0.26	*	Amphipoda	27.17
AH MR	A ES	0.33	*	Calanoida	23.55
AH MR	O MR	-	n.s.	Calanoida	25.33
AH ES	O MR	0.18	*	*C. maenas*	21.74
MR	**ES**	0.20	*	Amphipoda	22.20
3: Large, Autumn		-	n.s.		
T MR	T ES			Amphipoda	22.26
T MR	AH MR			Amphipoda	20.46
T MR	O MR			Amphipoda	15.7
T ES	AH MR			Amphipoda	25.48
T ES	O MR			Amphipoda	21.82
AH MR	O MR			Amphipoda	20.61
MR	**ES**	-	n.s.	Amphipoda	25.01
4: Large, Summer vs Autumn		0.093	*		
T MR	TMR	0.055	*	Calanoida	17.76
T ES	T ES	-	n.s.	Amphipoda	27.45
A MR	A MR	0.107	*	Calanoida	25.89
O MR	O MR	0.118	*	Calanoida	16.10

Table 4.4: SIMPER (AS % = percentage average similarity, relative contribution of prey types to the average similarity within each site, and total % contribution of the listed prey types) for the three groups of fish collected from saltmarsh sites within the Blackwater Estuary. T = Tollesbury, AH = Abbotts Hall, O = Orplands, MR = managed realignment, ES = established saltmarsh. Cal = Calanoida, Har = Harpacticoida, Bar = barnacle cyprid, Amp = Amphipoda, Car = *Carcinus maenas,* Cra = *Crangon crangon*, Ner = *Nereis* spp., Chi = Chironomidae, Ful = Fulgoromorpha

Sites	AS %	Prey types									Total
		Cal	Har	Bar	Amp	Car	Cra	Ner	Chi	Ful	
Small, Summer											
T MR	50	87		13							100
T ES	77	93									93
AH MR	82	74	24								98
AH ES	55	67	26								93
O MR	64	69	30								99
MR	57	87	11								98
ES	57	90	8								98
Large, Summer											
T MR	21	47	4		5	27		8			56
T ES	38				81	19					81
AH MR	31	71	18		6						95
AH ES	25				17	72	7				17
O MR	21	47	11				31	5			58
MR	21	73				8	5	6			92
ES	28				51	45					96
Large, Autumn											
T MR	18	11	32		20	13		15			62
T ES	24	17	14		64						95
AH MR	27	24	10		43				21		77
O MR	14	5	4		35	4		12	10	23	44
MR	13				40						40
ES	22				66						66

Figure 4.5: The proportion of prey types in ascending order of mean biomass, in the diets of large (30-59 mm) 0-group bass, collected from five sites in the Blackwater Estuary, in summer 2005-6 (number of bass = 141). MR = managed realignment, Established = adjacent established saltmarsh. The bubble size is proportional to the percentage of the prey type in the diet

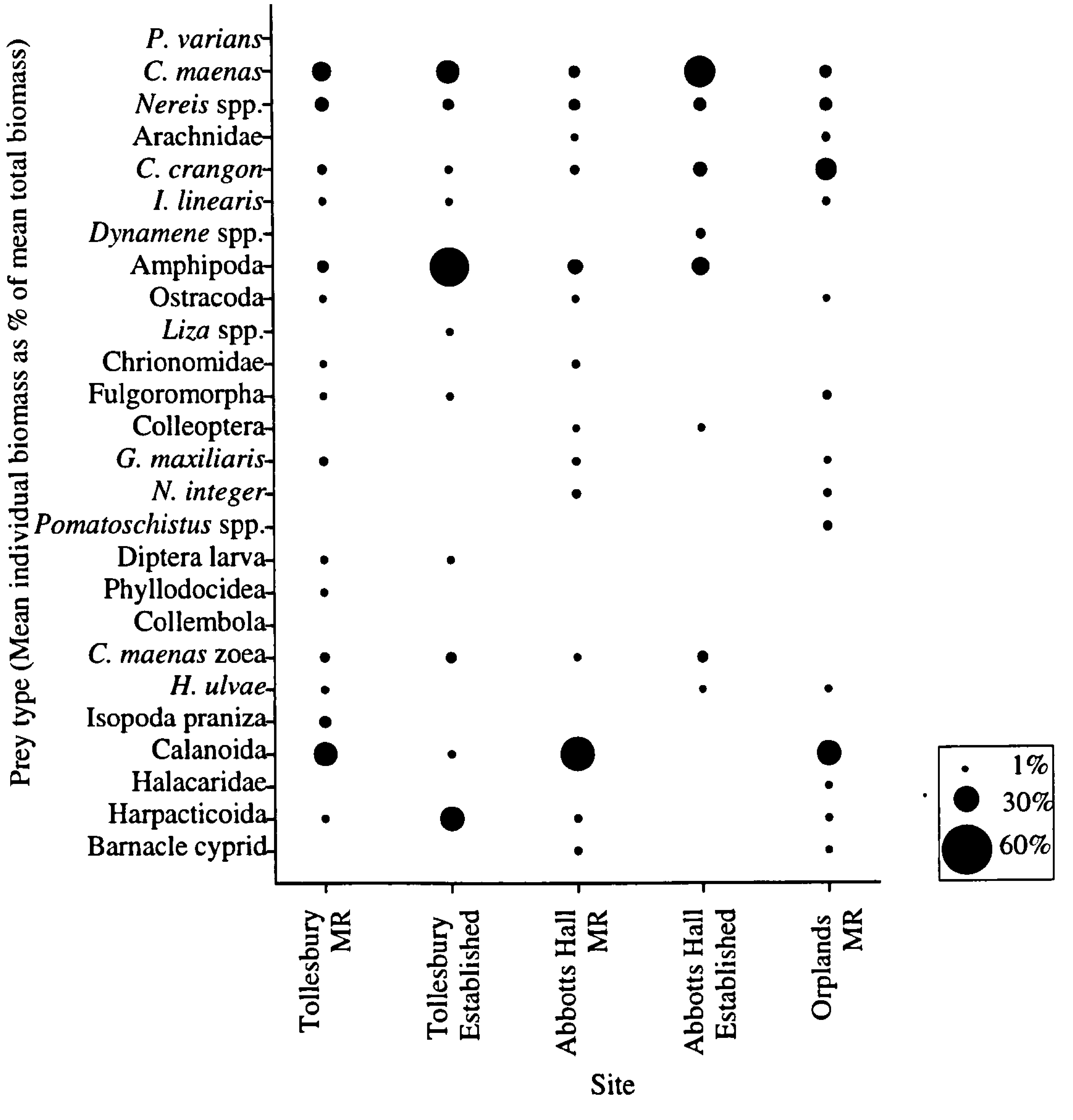
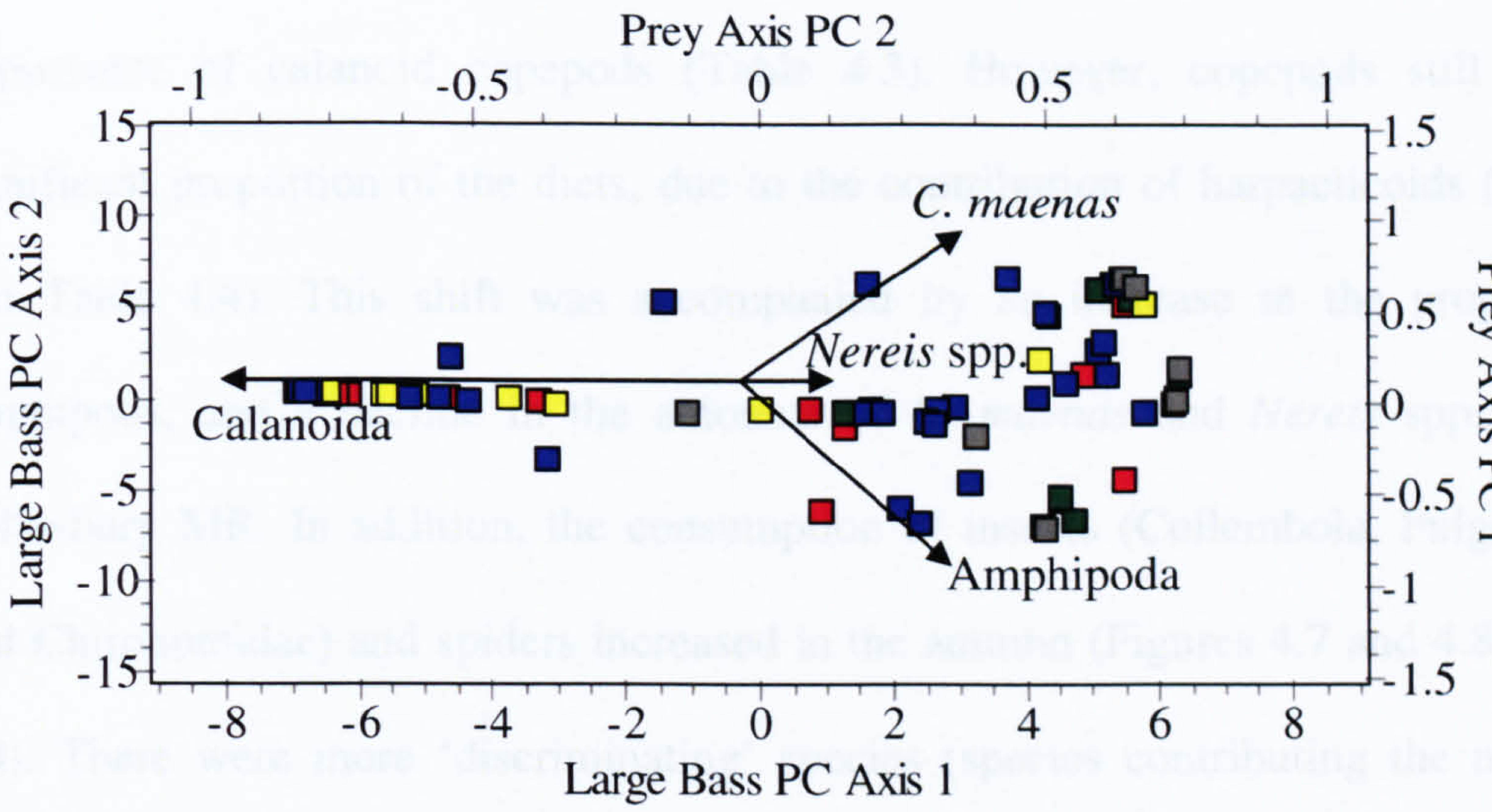


Figure 4.6: Covariance Principle Components (PC) Analysis of the diets of large bass (30-59 mm) in summer, leaving Abbotts Hall (red), established saltmarsh adjacent to Abbotts Hall (green), established saltmarsh adjacent to Tollesbury (grey), Tollesbury (blue) and Orplands (yellow) on the ebbing tide, in relation to prey type vectors (black arrows)



By autumn, there were no significant differences in the diets of large bass between the sites or between the managed realignments and the established saltmarsh (Figures 4.7 and 4.8, and Table 4.3). The diets of large bass leaving the realignment sites were significantly different from those in summer, mainly because of a reduction in the importance of calanoid copepods (Table 4.3). However, copepods still formed a significant proportion of the diets, due to the contribution of harpacticoids (Figure 4.7 and Table 4.4). This shift was accompanied by an increase in the proportions of amphipods, and a decline in the amounts of *C. maenas* and *Nereis* spp., except at Tollesbury MR. In addition, the consumption of insects (Collembola, Fulgoromorpha and Chironomidae) and spiders increased in the autumn (Figures 4.7 and 4.8 and Table 4.4). There were more 'discriminating' species (species contributing the most to the differences between the sites) in autumn than in summer at all sites because of the increased range of food types in individual fish and a reduced dependence on particular prey types. This was especially true at Orplands where three additional discriminating species more than in summer were identified.

The principal components analysis show that there was high within-site variation of the large 0-group bass caught in summer (Figure 4.6) unlike for small bass in summer or large fish in autumn (Figures 4.4 and 4.8) and this was due to the diets of individual fish being dominated by different prey types. For example, in some large bass, up to 100 % of the diet was comprised of calanoid copepods of which up to 718 individuals were consumed. Within the same group, other individuals only consumed *C. maenas* (up to ten individuals in one bass) or *C. crangon* (3-4 individuals in one bass). Some individuals only consumed *Nereis* spp. or Arachnidae; however, these prey items were large and only one individual was required to fill the stomach (to 8 % IR).

Figure 4.7: The proportion of prey types in ascending order of mean biomass, in the diets of large (30-59 mm) 0-group bass, collected from five sites in the Blackwater Estuary, in autumn 2005-6 (n = 160). MR = managed realignment, Established = adjacent established saltmarsh. The bubble size is proportional to the percentage of the prey type in the diet

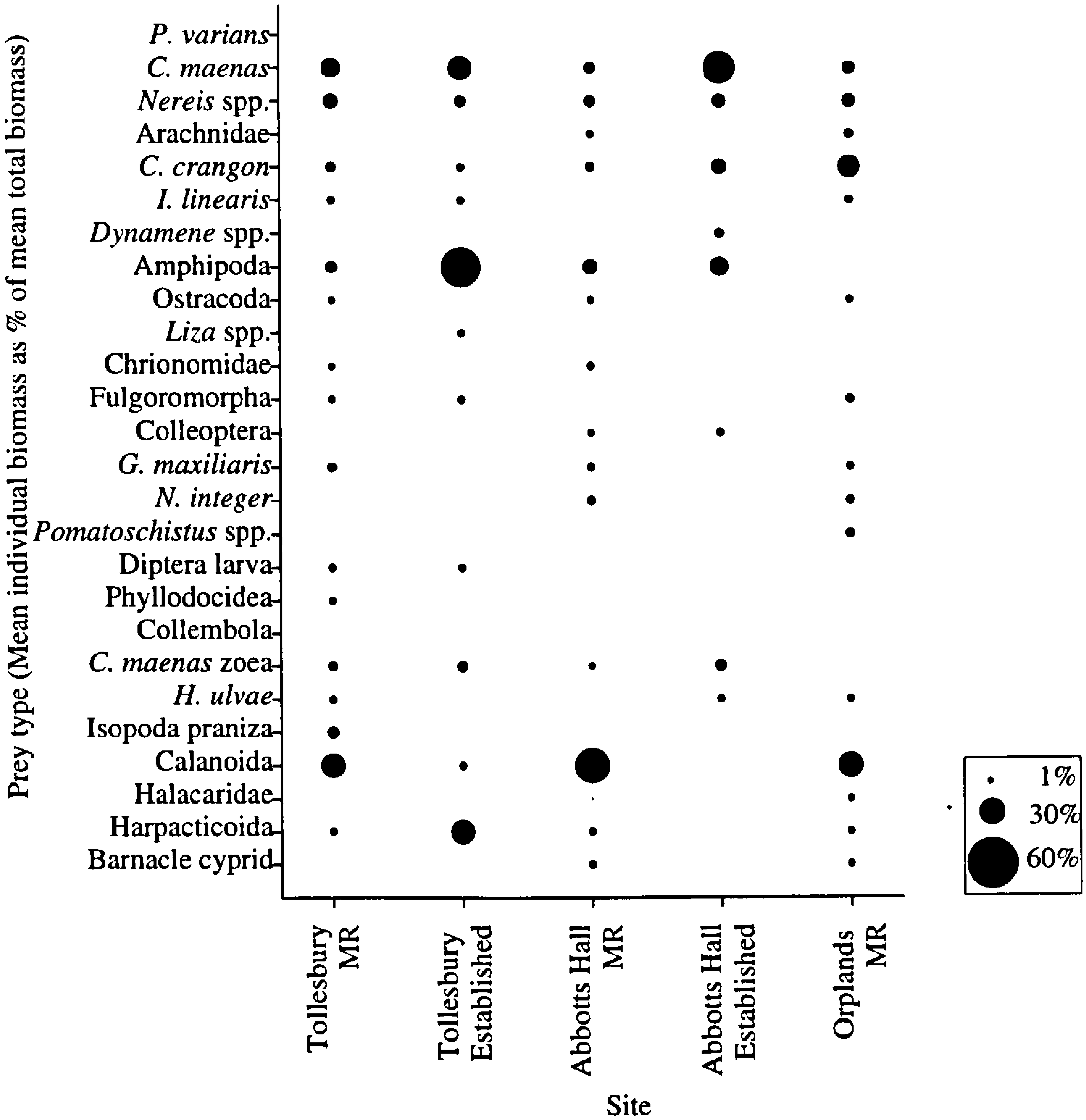
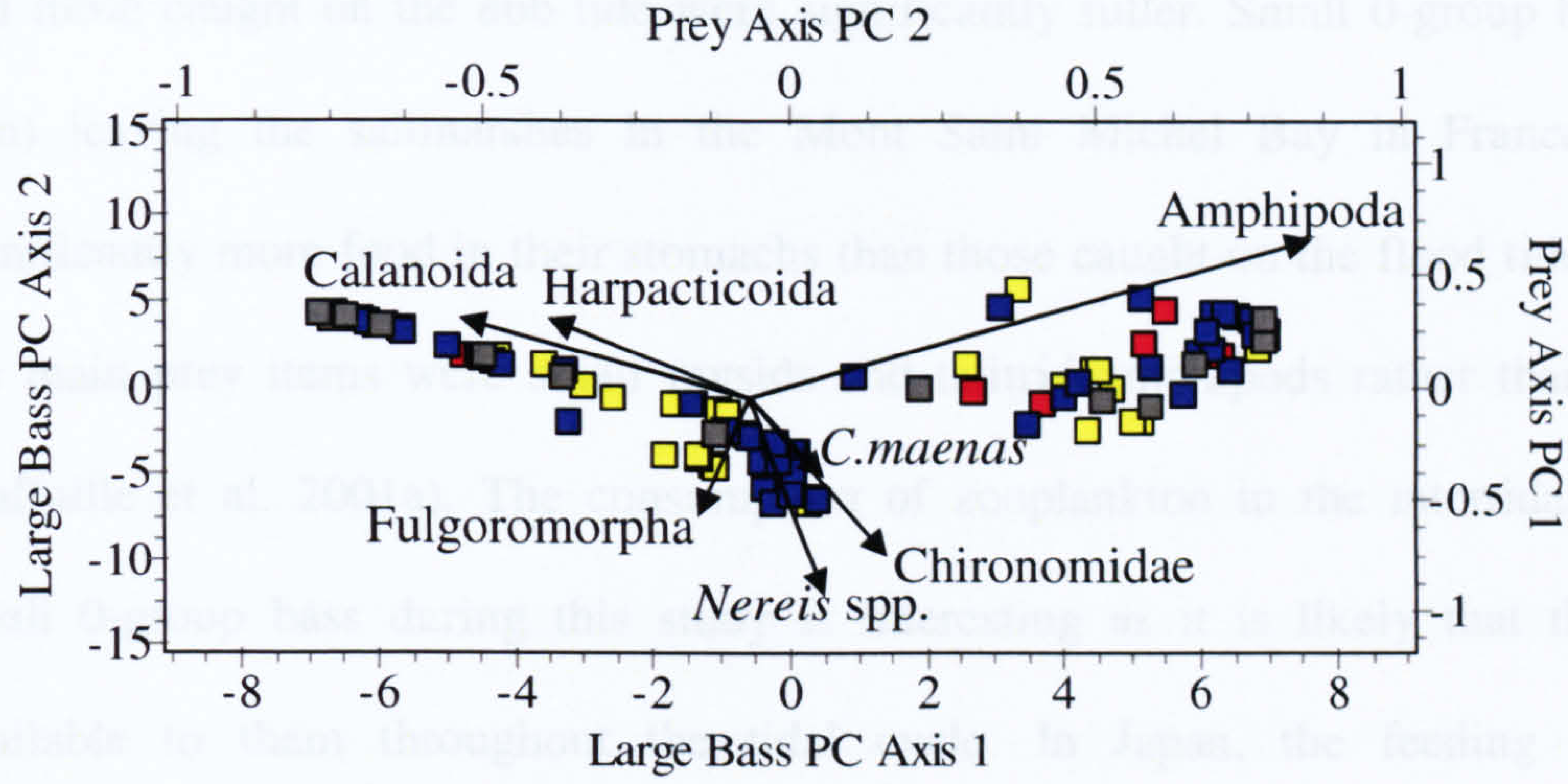


Figure 4.8: Covariance Principle Components (PC) Analysis of the diets of large bass (30-59 mm) in autumn, leaving Abbotts Hall (red), Tollesbury (blue), established saltmarsh adjacent to Tollesbury (grey), and Orplands (yellow) on the ebbing tide, in relation to prey type vectors (black arrows)



Discussion

The smallest bass (15-29 mm) fed predominantly when in all of these intertidal habitats as those caught on the flood tide had guts that were empty or with little food in them and those caught on the ebb tide were significantly fuller. Small 0-group bass (12-22 mm) leaving the saltmarshes in the Mont Saint Michel Bay in France also had significantly more food in their stomachs than those caught on the flood tide; however, the main prey items were small mysids and talitrid amphipods rather than copepods (Laffaille et al. 2001a). The consumption of zooplankton in the intertidal marsh by small 0-group bass during this study is interesting as it is likely that this food is available to them throughout the tidal cycle. In Japan, the feeding activity of zooplanktivorous postlarvae of the Japanese sea bass *Lateolabrax japonicus* was elevated within the flooding surf zone (Hibino et al. 2006). This was attributed to the increased resuspension and density of benthic copepods and it was also suggested that it is easier for bass to locate the zooplankton in shallower waters vertically, than in deeper waters, horizontally (Hibino et al. 2006).

In summer, at Tollesbury realignment and the two ancient saltmarshes there were significantly higher amounts of food in the larger 0-group bass caught on the ebb tide than in those entering the sites. The Tollesbury realignment site is relatively low, offering the fish a longer time to feed than at Orplands and Abbotts Hall. In addition at Tollesbury MR, the fish entering on the flood tide had relatively empty guts and this contributed to the significance of the difference with the ebb-caught fish.

The time required to digest large prey, especially those with calcareous exoskeletons, to a stage where they could no longer be identified, was not directly measured. Lancaster (1991) calculated a mean gut evacuation rate of 4.3 to 5 % h^{-1} for captive small 0-group

(26-45 mm) bass, but stated that this value is likely to be an underestimate, as the stress of captivity slows digestion. It is therefore possible that in the larger bass, the presence of some less easily digested large prey items from the previous tide may also have affected the tidal comparisons of gut fullness.

The results presented here for bass add to the body of work that has demonstrated that saltmarshes are important feeding habitats for the juveniles of large species. 33 % of the 0-group bass sampled by Laffaille (2001a) entered the saltmarshes with empty stomachs; the fish then foraged actively for one to two hours, and most (98 %) left with full stomachs. This is consistent with the current study in which 38 % of 0-group bass entered the saltmarshes with empty stomachs and 93 % left with full stomachs. In the eastern USA, the killifish IR increased with the residence time in saltmarshes (Kneib 1997) and the food intake during each two to three hour intertidal marsh access period was double that of fish restricted to subtidal areas (Madon et al. 2001). Juvenile *Fundulus heteroclitus* was also found to consume significantly greater amounts of food on the ebb tide than the flood tide; however, this occurred even when the high tide level was too low to provide fish access to the high marsh, and the fish were forced to remain within ditches (Allen et al. 1994).

The nursery function of intertidal estuarine habitats for fish has been attributed partly to refuge from predation (Hampel et al. 2005). Although no large piscivorous fish were caught in the saltmarshes during this study, piscivorous bass (30-40 cm long) were observed in the deep creeks of the natural marshes and at the seawall breaches of the managed realignment sites, becoming most active about two hours after high water on spring tides, catching prey that leave the realignments on the ebb tide. This observation is consistent with those of previous studies which suggest that creek mouths are preferred habitats for piscivorous fish (Simenstad et al. 1998; Colclough et al. 2005). For example piscivorous, striped bass *Morone saxatilis* (21-61 cm) tagged in Delaware Bay, were most abundant where their prey was most concentrated at creek mouths, tending to move up larger saltmarsh creeks during the ebbing tide to feed (Tupper and Able 2000). The relationship between the abundance of piscivorous fish and the bass mortality rate in saltmarshes is unknown but is thought to be important (Sheaves 2001). In this study, 0-group bass were observed entering these habitats in the shallow water at the front of the flood tide. It is possible that the 0-group bass feed mostly in these intertidal habitats because that is when they have large areas of turbid shallow water in which they can feed in relative safety from predatory fish. In contrast the channels and creeks of the estuary shelve rapidly and provide less shallow subtidal habitat for small bass.

In summer, copepods, particularly calanoids, were the preferred prey for the zooplanktivorous small bass (15-29 mm) in all sites and there was little variation between sites. The calanoid species present in the water column at the time of fish sampling included calanoid copepods (predominantly *Temora, Calanus*, and *Acartia* spp). Small bass also ate harpacticoid copepods, but this may not indicate a benthic feeding habit as zooplankton samples (250 μm net) showed these normally benthic copepods (predominantly *Tisbe furcata* and *Enterpina* sp.) were present in the water column and have been in a previous survey (Fox et al. 1990). The reason is not known but harpacticoids may be passively suspended from the benthos by small waves in the shallow water in the flood tide, where the small bass are common. Large 0-group bass (30-59 mm) in the managed realignment sites also ate mainly copepods, but in the saltmarshes, large bass consumed a greater proportion of epibenthic prey (living on the surface of the sediment), and hyperbenthic prey (living just above the surface of the sediment). By autumn, large bass generally consumed a greater proportion of hyperbenthic invertebrates, insects, and arachnids.

Although prey selectively was not assessed, as a quantitative study of prey availability was outside the scope of this study, the results presented here are generally consistent with the hypothesis that differences in the diets of juvenile bass are strongly related to the resident fauna of their habitats (Pickett and Pawson 1994). For example, the dominance of calanoids in the diets of small zooplanktivorous bass is a reflection of the fact that the Blackwater zooplankton community is generally dominated by calanoid copepods, particularly *Acartia* and their nauplii and harpacticoid copepods (Fox et al. 1990). The dominance of calanoids in the diets of 0-group bass as opposed to other zooplankters is significant because their relatively large size makes them easier to find for these visual feeders, even in turbid waters, and offers a higher net energy gain than smaller zooplankters (Hibino et al. 2006).

The ontogenetic dietary shift from zooplankton to epibenthic and hyperbenthic prey has been reported for older juvenile bass in western European waters (Kennedy and Fitzmaurice 1972; Aprahamian and Barr 1985; Kelley 1987; Hostens and Mees 1999; Laffaille et al. 2001a; Hampel et al. 2005) and for other species of fish in similar shallow coastal ecosystems (Baldo and Drake 2002; Galarowicz and Wahl 2005; Islam and Tanaka 2006). The shift from zooplankton to epi- and hyperbenthic prey occurred in summer in the established saltmarshes and more clearly in autumn within the managed realignment sites, although copepods were still present in the diets at all sites in autumn. The continued consumption of zooplankton by large 0-group bass did not result in the fish eating less overall, and simply reflects the opportunistic nature of the feeding behaviour of 0-group bass.

The importance of epi- and hyperbenthic prey in the diets of juvenile bass has been reported previously (Aprahamian and Barr 1985; Lancaster 1991; Maes et al. 2003; Sa et al. 2006). During the current study, mysids were not a significant component of the diet despite them being common in samples previously collected from the Blackwater Estuary (Fox et al. 1990) and being consumed by 0-group bass in a previous study (Lancaster 1991). Laffaille (2001a) found mysids in the guts of bass caught on the flood tide, but not on the ebb, because mysids were more commonly encountered subtidally than in the saltmarshes. Despite mysids migrating with the tide (Speirs et al. 2002) in this study mysids were not a notable component of the zooplankton samples possibly because they tend to be nocturnal. Laffaille (2001a) also stated that the rapid digestion and evacuation of mysids consumed subtidally, explains a lack of mysids in the guts of bass collected on the ebbing tide. Highly motile benthic invertebrates were important in the diets of fish leaving the sites including gammarid and talitrid amphipods and to a lesser extent, *C. crangon*. This finding is consistent with that from the Mont Saint Michel Bay, France, where 0-group bass collected on the ebbing tide had also mainly consumed amphipods (Laffaille et al. 2001a).

In a study on the Hudson Estuary, Howe et al., (2008) showed that gammarids were the preferred prey type for striped bass *Morone saxatilis*. The low consumption of amphipods at Tollesbury MR compared with the adjacent saltmarsh, is consistent with a presence of amphipods within the managed realignment site and absence outside it in the ancient saltmarsh (Reading et al. 2008).

There was a significant difference between the diets of large 0-group bass collected in summer from the managed realignments and the established saltmarsh, but not in the other two groups (small bass or large bass in autumn). However, epibenthic prey (*C. maenas* and *Nereis* spp.) were more regularly consumed both at Tollesbury managed realignment and both the saltmarsh sites than in Abbotts Hall and Orplands managed realignment sites. This consumption is also likely to be a function of prey availability as there is a relatively high abundance of benthic invertebrates at Tollesbury MR (Reading et al. 2008). The other two sites have developed predominantly into vegetated saltmarsh where benthic invertebrates are less abundant (English-Nature 2005; Paramor and Hughes 2005). The fact that the ancient saltmarshes are vegetated indicates that the fish fed in the creeks.

The importance of crabs in the diets of juvenile bass has been reported elsewhere (Aprahamian and Barr 1985; Kelley 1987) and is thought to be more common in UK coastal environments than in France, Italy or Ireland (Pickett and Pawson 1994). *C. maenas* was particularly important in the diets of bass in summer but not in autumn. This may reflect a decline in abundance or growth of the crabs to sizes too large for 0-group bass to consume. Small, growing crabs undergo periods of ecdysis (carapace shedding) and during this time they may be easier for bass to consume and digest than bigger crabs with stronger, regenerated carapaces. In the Westerschelde Estuary juvenile *C. maenas* appeared in the saltmarsh creeks in June (3 mm mean carapace width) but had grown to 30 mm by winter, when they migrated out of the marshes (Cattrijsse et al. 1994).

In summer, the majority of large 0-group bass consumed over 90 % of one particular prey type some fed predominantly on calanoid copepods and others on *C.maenas* and amphipod prey. This feeding specialisation could reflect a learnt behaviour, with bass specialising more in summer than in autumn because of changes in the available prey types or feeding cues (Warburton 2003; Stoner 2004). It could also be because of seasonally high, but patchy, prey abundance. Further research is required to explain this trend.

By autumn, this reliance on one prey type was less evident, possibly because of the availability of a higher range of prey types. The importance in autumn of prey of terrestrial origin or those associated with the strandline (talitrid amphipods), is evident. Vegetated habitats are known to provide more niches and refugia for some potential prey types. For example, vegetated habitats in the supralittoral offer greater structural complexity than less vegetated habitats and have been correlated to increased invertebrate diversity of aquatic and terrestrial arthropods including Collembola, Talitridae, and Chironomidae (Attrill et al. 1999; Romanuk and Levings 2003). The importance of herbivorous (e.g. Fulgoromorpha) and detritivorous (e.g. Chironomidae) insects in the diets of juvenile fishes (3-10 cm) has been reported previously for bass (Labourg and Stequet 1973) and other species (Allen et al. 1995) and forms an important addition to the seasonal transfer of energy to the Blackwater Estuary.

The increased consumption of insects by large bass in autumn may be explained by their increased availability or by the absence of alternatives (e.g. small crabs). The abundance of Diptera in strandline cores collected in saltmarshes along the Essex coast was greater in autumn than in summer (Mason et al. 1991). McIvor and Odum (1998) stated that small juvenile fishes in the eastern US prefer shallow depositional habitats at low tide for the consumption of benthic invertebrates and only move onto the vegetated marsh surface to seek refuge. In contrast Weisberg et al., (1981) showed that killifish *Fundulus hereroclitus* enter the vegetation to feed whenever possible although the feeding activity is greatest during high tides regardless of marsh inundation. Laffaille et al. (2001b) showed that bass in the Mont Saint-Michel Bay colonised intertidal saltmarsh creeks for 43 % of the tides, but that foraging in the vegetated flat occurred rarely as these habitats are only flooded by 5 % of the tides. Cattrijsse et al (1994) also suggest that that the vegetation in saltmarshes is rarely used by juvenile fishes. It would be interesting to determine whether the spiders and insects are consumed at the surface of the water, within the vegetation, after being washed into the creeks, or via a combination of these pathways.

As gut contents analysis provides an accurate snapshot of trends in ingestion of prey, there is a need to consider the energy assimilated on larger spatial and trophic scales (Boesch and Turner 1984). This is addressed in the following chapter, through the use of stable isotope tracers.

In conclusion the three different realignment sites and two ancient marshes provide valuable but different feeding opportunities for all sizes of 0-group bass. Tollesbury MR and the two ancient saltmarshes have a greater feeding value to large 0-group bass than the other two managed realignment sites. This is because they allow for a relatively longer feeding time in the creeks and provide greater densities of benthic prey in the soft sediments than in the higher vegetated sites of Orplands and Abbotts Hall MR. This is important information for habitat recreation because it shows that during the period of fastest growth (summer), 0-group bass benefit greatly from habitats with deep creeks and soft sediments. However, while these differences are important to this recreationally and commercially important species at one of its most vulnerable life stages, by autumn, they are mitigated by the opportunistic nature of 0-group bass feeding.

Chapter 5: Sources of primary productivity and the trophic levels of fishes in three managed realignment sites in the Blackwater Estuary

Introduction

Many saltmarshes around the world are disappearing (Harty and Cheng 2003; Knogge et al. 2004). In SE England this rate of loss has been particularly high (Burd 1992; Cooper et al. 2001; van der Wal and Pye 2004) at 2 % per year (Dixon et al. 1998). The loss of vegetation is likely to deprive consumers of sources of primary productivity and habitats in which to feed. The impact of past and future saltmarsh loss on fish and invertebrate consumers may vary over a short spatial scale (Svensson et al. 2007) and the exact ecological consequences of this loss in SE England are currently unknown.

The importance of saltmarsh vegetation as a source of primary productivity to saltmarsh invertebrates has been stressed by several authors (Teal 1962; Creach et al. 1997; Kwak and Zedler 1997; Carlier et al. 2007). Some saltmarsh plants are consumed directly by herbivorous talitrid amphipods and insects (Boorman 2000). In Essex, saltmarshes are dominated by *Puccinellia maritima* and *Atriplex portulacoides* (Burd 1992). These species form dense stands making it difficult for fishes and macroinvertebrates to move amongst them. Saltmarsh vegetation normally enters the food web indirectly in detrital form after varying degrees of microbial breakdown (Currin et al. 1995; Boorman 2000; Fry 2006). There is growing evidence to indicate that phytoplankton, microphytobenthos (MPB) and green algae, which are smaller, easier to consume and more nutritionally valuable than detritus, form the main sources of primary productivity in some saltmarsh food webs (Sullivan and Moncreiff 1990; Riera and Hubas 2003;

Moens et al. 2005; Galvan et al. 2008). In particular, these organisms have been shown to contribute more to the diets of infauna, mud snails and crabs than fresh or detrital saltmarsh plants (Riera et al. 1999; Herman et al. 2000; Galvan et al. 2008).

In some areas of SE England, the existing line of flood defence has been moved landwards to protect the land behind the new defence from the increased threat of flooding due to rising sea levels. This process called 'managed realignment' may result in the development of saltmarshes. In contrast to the eroding natural saltmarshes, some managed realignment areas contain more extensive pioneer zones that are dominated by succulent halophytes such as *Salicornia europaea* and *Suaeda maritima* (Paramor and Hughes 2005). These plants are less dense and may offer fishes a habitat in which to feed where their predation risk is less than on adjacent mudflats. Food webs in managed realignment sites may therefore be different from each other and from those in natural saltmarshes, and an understanding of these differences may be useful in designing future realignment schemes.

Stable isotope analysis

Stable isotope ratio analysis is routinely used in the study of food webs (Fry 1988; Currin et al. 1995; Melville and Connolly 2003). The isotope values of primary producers and consumers are used to identify the sources of primary production at the base of food chains and to determine the trophic levels of consumers within them (Peters et al. 1978; Fry and Sherr 1984; Peterson and Fry 1987; Vander Zanden and Ransmussen 1999). The technique is particularly useful when gut contents analysis cannot be performed; for example, when insufficient organisms are available for gut contents analysis, when the majority of guts are empty, or when the prey are too macerated or digested to be identified (Grey 2006). Unlike gut contents analysis, stable isotope analysis also provides a time-integrated measure of food assimilation (Wainright et al. 1993). However, where possible, stable isotope analysis and gut contents analysis should be combined to describe the structure of food webs more accurately (Layman et al. 2007).

Stable isotope analysis is the study of the relationship between the most commonly occurring stable isotopes of carbon and nitrogen (^{12}C and ^{14}N) and two rarer, heavier isotopes (^{13}C and ^{15}N). The stable isotope ratios use the delta notation ($\delta^{13}C$ or $\delta^{15}N$) which relates the proportion of the ratio of the heavy to light isotopes (in this study ^{13}C:^{12}C or ^{15}N:^{14}N) in the sample, to the ratios in the international standards (Vienna Pee Dee Belemnite in the case of carbon, and atmospheric air in the case of nitrogen). See the methods section below for more details. The ratio of the stable isotopes of carbon (^{13}C:^{12}C) varies at the base of the food web and reflects the sources of primary productivity in consumers, with an average enrichment of 1 ‰ per trophic level (DeNiro and Epstein 1978; Fry and Sherr 1984). The ratio of the stable isotopes of nitrogen (^{15}N:^{14}N) exhibits an average stepwise enrichment of approximately 3.4 ‰ with each trophic level (DeNiro and Epstein 1981; Minagwa and Wada 1984).

Factors affecting the $\delta^{13}C$ values of photosynthetic organisms

Three main factors affect the $\delta^{13}C$ stable isotope values of photosynthetic organisms: the $\delta^{13}C$ of the external carbon source, the fractionation during carbon uptake and the fractionation during CO_2 respiration. The carbon sources for photosynthetic organisms in saltmarshes are predominantly atmospheric carbon dioxide (CO_2) and seawater bicarbonate (HCO_3^-). The $\delta^{13}C$ values of HCO_3^- are more enriched than for CO_2 due to a preferential retention of ^{13}C in HCO_3^-, therefore species which are restricted to using

CO_2 as the only carbon source have more depleted $\delta^{13}C$ values than species that also use HCO_3^- (O'Leary 1981; Keeley and Sandquist 1992; Finlay and Kendal 2007). The $\delta^{13}C$ values of atmospheric and dissolved CO_2 vary seasonally and with temperature (Keeley and Sandquist 1992). The majority of photosynthesis by saltmarsh vascular plants occurs while the plants are emersed and exposed to atmospheric CO_2 (Silva et al. 2004) because in water there is a relatively low concentration of CO_2 and a slow diffusion rate.

The $\delta^{13}C$ values of plants are affected by the fractionation during carbon uptake which is determined by the rate of CO_2 supply and the rate of assimilation (Finlay and Kendal 2007). Factors affecting the rate of CO_2 supply include cell membrane or stomata permeability and the flux of CO_2. The CO_2 flux is determined by ambient CO_2 concentrations; CO_2 concentrating mechanisms which affect the ability to discriminate against ^{13}C; and water flow which affects the thickness of the CO_2 boundary layer (Keeley and Sandquist 1992).

The rate of carbon assimilation is determined by the type of metabolic pathway for carbon fixation: C_3 (Calvin), C_4 (Hatch-Slack), and Crassulacean Acid Metabolism (CAM) (Marshall et al. 2007). In the C_3 metabolic pathway, CO_2 is carboxylated by ribulose-1, 5-bisphosphate carboxylase-oxygenase (RUBISCO) to the C_3 compound phosphoglycerate, causing relatively depleted $\delta^{13}C$ values in C_3 plants (Boutton 1991; Marshall et al. 2007). Saltmarsh plants that use the C_3 photosynthetic pathway include *Salicornia, Limonium*, *Suaeda*, *Puccinellia* and *Atriplex.* Phytoplankton use bicarbonate as a carbon source and follow a modified C_3 metabolic pathway involving β-carboxylation (Boutton 1991). The carbon fractionation during carbonate production is low, whereas the fractionation during the uptake of dissolved inorganic carbon is higher, resulting in phytoplankton $\delta^{13}C$ values of -19 to -24 ‰ (Fry 2006). Most aquatic macrophytes such as *Ulva* spp. follow the C_3 photosynthetic pathway, and are also able to concentrate CO_2 using HCO_3^- (Beer and Shragge 1987; Madsen and Sand-Jensen 1991) which can result in depleted, intermediate or enriched $\delta^{13}C$ values.

In the C_4 pathway, plants use phosphoenolpyruvate carboxylase (PEPC) to convert phosphoenolpyruvate (PEP) into a C_4 compound, either malic acid or aspartic acid, which is then decarboxylated to CO_2 (Boutton 1991; Marshall et al. 2007). Since the substrate for PEPC is HCO_3^- rather than CO_2, an additional fractionation step is present in C_4 plants (O'Leary 1981). The CO_2 accumulates to high concentrations and it is then fixed by RUBISCO via the Calvin cycle as with C_3 plants (O'Leary 1992; Marshall et al. 2007). The C_4 pathway contributes less to isotopic fractionation, therefore C_4 plants such as *Spartina* are relatively enriched in $\delta^{13}C$ (5‰ compared with -28‰ in C_3 plants). Diatoms such as *Thalassiosira* follow the C_4 pathway to store CO_2 during low light levels, resulting in intermittently enriched $\delta^{13}C$ values (Reinfelder et al. 2000).

In the CAM pathway, plants produce malate from CO_2 through the C_4 pathway and it is stored overnight. The carbon is then released from the malate during the day and fixed by RUBISCO via the C_3 pathway (Marshall et al. 2007). This process results in intermediate carbon isotope values (Madsen and Sand-Jensen 1991).

Finally, fractionation during photorespiration has been shown to increase and decrease the $\delta^{13}C$ value (O'Leary 1981). However CO_2 respiration causes minimal fractionation (Peterson and Fry 1987).

Factors affecting the $\delta^{15}N$ values of photosynthetic organisms

Three factors affect the $\delta^{15}N$ stable isotope values of photosynthetic organisms. These are the $\delta^{15}N$ of the nitrogen source; the fractionation during nitrogen uptake; and the fractionation during nitrogen excretion. Most nitrogen is present as nitrogen gas (N_2) in the atmosphere but this is not available to plants directly. Sources of nitrogen used by primary producers include nitrate (NO_3^-), ammonium (NH_4^+) and dissolved organic nitrogen (Marshall et al. 2007). The $\delta^{15}N$ of N_2 is 0 ‰ as it is the standard to which other sources are compared. The $\delta^{15}N$ signatures of NO_3^- and NH_4^+ vary greatly (-20 to 10 ‰) due to biogeochemical processes such as denitrification (the reduction of NO_3^- to N_2), nitrification (the oxidation of ammonia into nitrite and then nitrate), and biological uptake (Fry 2006). The fractionation resulting from the uptake of NO_3^- during denitrification increases with increasing NO_3^- availability, reduced light levels, the growth rate of denitrifying bacteria, and reduced C-sources relative to N-sources (Wada 1980; Needoba et al. 2004). The fractionation during uptake of NH_4^+ is sensitive to pH and ambient concentrations (Yoneyama et al. 2001). At high NH_4^+ concentrations (>1000 $\mu m.l^{-1}$), uptake of NH_4^+ is caused by passive membrane diffusion of NH_3 catalysed by GDH (glutamate dehydrogenase). At low NH_4^+ concentrations (<100 $\mu m.l^{-1}$), NH_4^+ is transported actively and then assimilation is catalysed by GS (glutamine synthetase) (Hoch et al. 1992). The preferential excretion of ^{14}N rich compounds, such as NH_4^+, results in the enrichment of $\delta^{15}N$ values of the remaining tissues (Yoneyama et al. 2001). These processes of fractionation make it possible to trace the ^{15}N and ^{13}C pathways in organisms though the food chain.

Aim

The aim of the study was to determine the sources of primary productivity and the route of transfer of organic matter up the food chain to fishes in the managed realignment sites at Tollesbury, Abbotts Hall and Orplands. The study places particular emphasis on 0-group *Dicentrarchus labrax* (L.) a commercially important species which is abundant during the summer, but data for *Atherina presbyter*, *Pomatoschistus microps*, *Liza ramada* and *Sprattus sprattus* are also considered.

Methods

Field sampling

Field sampling was carried out at Tollesbury, Abbotts Hall and Orplands managed realignment sites (See Chapter 2 for site descriptions). Sampling for stable isotope analysis was conducted in July 2007 and fish were collected for gut contents analysis on spring tides between 2005 and 2007 (see Chapter 2 for fish collection methods).

Suspended particulate organic material (POM) / phytoplankton

A 55 μm mesh phytoplankton net and a 250 μm mesh zooplankton net were towed three times for five minute periods on the flooding and ebbing tide, around high tide ($\pm$ 1 hour) at the breach in the sea wall, on the same days as the fish were caught. The phytoplankton samples were then filtered through a 250 μm mesh and the zooplankton samples were filtered through a 500μm mesh to remove larger sized fractions. Examination of the remaining 'phytoplankton' (55-250 μm) and 'zooplankton' (250-500 μm) samples showed them to be predominantly suspended particulate organic matter (hereafter referred to as POM), rather than phytoplankton and zooplankton, respectively. This POM may consist of a mixture of living and dead phytoplankton, bacteria, plant detritus, zooplankton faecal pellets and benthic marine algae. The 55-250 μm and 250-500 μm POM samples were transferred to amber bottles to prevent further photosynthesis.

Plants and strandline detritus

Fresh leaves from several C_3 plant species (*Atriplex portulacoides*, *Limonium vulgaris, Salicornia europaea*, *Puccinellia maritima*) and the C_4 species *Spartina anglica* were collected from the three managed realignment sites as were fronds of the green algae *Ulva* spp. To assess variation within the C_3 plant community in more detail, specimens of *Limonium vulgaris*, *Suaeda maritima* and *Puccinellia maritima* were also collected from the saltmarsh adjacent to Abbotts Hall managed realignment site. All leaves and fronds were scraped clean of epiphytes prior to processing. Plant detritus was collected from the strandline debris deposited by the highest tide.

Microphytobenthos (MPB)

Microphytobenthos samples, predominantly epipelic diatoms, were scraped from the surface of the sediment with a scalpel in the three managed realignment sites. The samples were taken from areas where brown diatomaceous films were clearly visible. Care was taken to exclude as much non-microphytobenthos material as possible (as recommended by Sullivan and Zedler 1999).

Sedimented organic material (SOM)

Surface sediment scrapes without visible benthic diatomaceous films were also collected for sedimented organic material (SOM) from the three managed realignment sites and the established saltmarsh adjacent to Abbotts Hall managed realignment site. Microscopic examination of these samples confirmed that diatoms were not common in them.

Fishes and invertebrates

Bass, *Dicentrarchus labrax,* sand smelt, *Atherina presbyter*, gobies, *Pomatoschistus* spp., mullet *Liza* spp. and sprat *Sprattus sprattus*, were collected on the ebbing tide from the three managed realignment areas. See Chapter 3 for fish identification methods. Individuals of prey taxa were collected from each managed realignment site on the same days as the fishing. Talitrid and gammarid amphipods, and isopods were collected from amongst the strandline detritus; prawns, shrimps, ctenophores and cuttlefish from the net used to catch the fish; polychaetes from within the sediment; and crabs and terrestrial invertebrates from within the vegetation. Specimens were killed and frozen as soon as possible after collection as freezing does not affect the stable isotope values significantly (Sweeting et al. 2004).

Gut contents analysis

The gut contents of *Dicentrarchus labrax*, *Atherina presbyter*, *Pomatoschistus microps*, *Liza ramada* and *Sprattus sprattus* collected from the saltmarshes (July 2005-August 2007) were analyzed. See Chapter 4 for details of the gut contents analysis methods.

Stable isotope sample preparation

The samples were prepared using sterile techniques to minimise the risk of sample contamination. This included the use of powder-free latex gloves and acetone for cleaning all equipment between samples.

Microphytobenthos scrapes were laid out on clean shallow trays (1 cm depth), covered with a clean 55 μm mesh and illuminated whilst being moistened with filtered seawater (0.2 μm) for 3-5 hours. During this period, the diatoms formed a dense, visible mat on the surface of the mesh. The sample was then carefully collected onto a glass cover-slip and the presence of diatoms was confirmed by microscopy. Only small quantities of detritus and no animals were observed. The samples were placed onto previously combusted and weighed cores of glass fibre filter papers (Whatman GF/F) (6.25 % of total filter paper). The cores were then dried and reweighed.

POM samples were diluted to 40 ml with filtered seawater. 10 ml of the POM sample was retained for identification (see below). The remaining 30 ml was then filtered onto a pre-ashed (565 °C, 8 hrs) glass fibre filter paper (Whatman GF/F), under a gentle vacuum until the filter became clogged. The papers were dried (60 °C for 24 hrs), cut in half, and each half was weighed. To remove inorganic carbonates, one half of the filter paper sample was subjected to vapour acidification using concentrated HCl (12 M). It was then re-dried (60 °C for 24 hr), and re-weighed (following the methods of Hedges and Stern 1984; Ryba and Burgess 2002). The inorganic carbon content was measured gravimetrically by comparing the sample weights before and after acidification (Pinnegar and Polunin 1999). The other half of the filter paper sample was used for the analysis of total nitrogen content and $\delta^{15}N$. Two small (5 mm diameter) cores were removed from each filter half using a corer, each representing 6.25 % of the total filter paper weight. Cores were then placed into a tin capsule for isotope analysis.

White muscle tissue was dissected from the fishes as it is less variable in terms of $\delta^{13}C$ and $\delta^{15}N$ than other tissue types (Pinnegar and Polunin 1999). Calcareous exoskeletons were removed from the macroinvertebrates where possible and muscle tissue was dissected out when the sample was large enough. All tissue samples were dried at 60 °C until there was no further weight loss.

To remove inorganic carbonates from potential prey and sediment, half of each sample was decalcified for 12 hours in 1 M HCl, re-dried and then ground to a fine powder using a pestle and mortar following the method of Hedges and Stern (1984). These samples were processed in parallel to unacidified samples which were analysed for $\delta^{15}N$ to avoid enrichment of ^{15}N through the acidification process (Pinnegar and Polunin 1999). Samples were prepared as quickly as possible to prevent decay or contamination. Lipids can cause ^{13}C enrichment; however, lipid extraction techniques on fatty specimens may affect the $\delta^{15}N$ values (Sotiropoulos et al. 2004; Sweeting et al. 2006).

However, the separate analysis of samples for $\delta^{15}N$ and $\delta^{13}C$ before and after lipid extraction could not be performed in addition to the acidification procedures because of the small samples available.

The remaining 10 ml of POM (the subsample) was agitated to form a homogenous solution. The 'phytoplankton' subsamples were fixed and preserved in three drops of Acid Lugol's solution and the 'zooplankton' subsamples were fixed and preserved in 10 ml of 4 % formalin for later identification of the fauna. Each subsample was placed in a haemocytometer to identify and enumerate the organisms by use of a stereomicroscope.

Since few zooplankters were collected in the zooplankton nets, zooplankters for isotope analysis were sampled from the stomachs of small (25-30 mm) *D. labrax*. Undigested zooplankters were used and those in the hindgut were not used as digestion may affect isotope values (Guelinckx et al. 2008). These were calanoid copepods (predominantly *Temora, Calanus, Acartia* spp.). Benthic harpacticoid copepods (predominantly *Tisbe furcata* and *Enterpina* spp.) were also collected in this way from *D. labrax* and from small (20-29 mm) *P. microps.* Sampling in this manner ensured that the samples reflected the diet more accurately (Fry 1988; Sholto-Douglas 1991; Grey et al. 2002; Guelinckx et al. 2006). However, because the zooplankters were already dead it was not possible to purge their guts (Feuchtmayr and Grey 2003).

Non-filter paper samples were dried to a constant weight and ground to a fine powder using a pestle and mortar. Approximately 1 mg of each ground sample was placed into an ultra-clean 8 x 5 mm, tin capsule for subsequent isotope analysis.

Carbon and nitrogen stable isotope analysis

The organic carbon and nitrogen content and stable isotope values were measured, using an elemental analyser (ThermoFinnigan TC/EA Flash 1112, Bremen, Germany) coupled to a continuous flow isotope mass spectrometer (CF-IRMS) (ThermoFinnigan Delta Plus, Bremen, Germany). The standard delta (δ) notation (McKinney et al. 1950) in units of permil (‰), was used according to the formula:

$$\delta X = (R_{sample} / R_{standard} - 1) \times 1000 \qquad \textbf{(5.1)}$$

where X = heavy isotope (e.g. ^{15}N or ^{13}C);

$R = {}^{13}C{:}{}^{12}C$ for carbon and $^{15}N{:}^{14}N$ for nitrogen

All delta values are reported relative to Vienna Pee Dee Belemnite (vPDB) for carbon and to atmospheric N_2, for nitrogen, according to the formulae:

$$R_1 = R_{international\ ref.} * (\delta_2 + 1000) / (\delta_1 + 1000) \qquad \textbf{(5.2)}$$

and

$$\delta_4 = (\delta_3 + 1000) \times (R1 / R\ \text{international ref}) - 1000 \qquad \textbf{(5.3)}$$

where, for carbon:

R_1 = ratio of ^{13}C: ^{12}C of PDB (0.01122203);

$R_{international\ ref.}$ = ratio of ^{13}C: ^{12}C in the international reference (0.011185);

$\delta_1 = \delta$ reference compound (sucrose) vs. 'electronic PDB' (-13.7348 $\pm$0.103 SD);

$\delta_2 = \delta$ reference compound (sucrose) vs. PDB (-10.47 $\pm$ 0.13 SD)'

$\delta_3 = \delta$ of sample measured on mass spectrometer (versus 'electronic PDB');

δ_4 = corrected sample of $\delta^{13}C_{PDB}$

and, for nitrogen:

R_l = ratio of ^{15}N: ^{14}N of the N_2 cylinder (0.0036765);

$R_{\text{international ref.}}$ = ratio of ^{15}N:^{14}N in the international reference (0.0036765);

$\delta_1 = \delta$ reference compound (Ammonium sulphate) vs. N_2 cylinder (1.289 $\pm$ 0.07 SD);

$\delta_2 = \delta$ reference compound vs. N_2 in air (0.4 $\pm$ 0.3 SD);

$\delta_3 = \delta$ of sample measured on mass spectrometer (versus N_2 cylinder);

δ_4 = corrected sample of $\delta^{15}N_{air}$

Replicates of National Institute of Standards and Technology (NIST) standards of sucrose (carbon) and ammonium sulphate (nitrogen) were used to calibrate each new oxidation column. Calibration was also carried out for each sample run, using a range of urea standards for the determination of carbon and nitrogen content. Cicloesanone-2, 4-dinitrofenilidrazone ($C_{12}H_{14}N_4O_4$) was also processed as a solid internal working standard after every ten samples to monitor column performance and to correct for drift in isotope values. The experimental internal precision, which was calculated using the replicates of the internal standard, was $\pm$ 0.2 ‰ for ^{15}N and $\pm$ 0.1 ‰ for ^{13}C.

Data analyses

No lipid correction factor was applied to the data (Kiljunen et al. 2006). All values presented are the mean $\pm$ 1 standard deviation, except in those cases where only one sample was collected. The data were tested for normality using the Anderson-Darling test. Where there were more than two samples collected, the differences between their means were tested using a one-way ANOVA and where significant, followed by a post-hoc Tukey's pairwise comparison test.

Food quality

The percentage of organic carbon or nitrogen was calculated per sample using the formula:

$$\% \text{ organic C or N} = (\text{mass} / (\text{sample weight} - \text{core weight}))*100 * (\text{Wf} / \text{Wo}) \qquad \textbf{(5.4)}$$

Where, for organic carbon:

W_0 = initial sample weight before acidification to remove inorganic carbonates

W_f = final sample weight after acidification

C:N ratios were calculated using the percentage organic carbon and percentage nitrogen values to estimate the proportion of detritus in the samples.

Trophic position and fractionation

The trophic position of a consumer is a non-integer value that represents the energy-weighted number of trophic energy transfers leading to a consumer (Vander Zanden and Ransmussen 1999). The trophic position of a consumer can be calculated using the $\delta^{15}N$ of the consumer and its presumed basal resource. The consumers were assumed to have a $\delta^{15}N$ trophic enrichment of 3.4 ‰ above that of their diet (after Minagwa and Wada 1984; Fry 2006; Sweeting et al. 2007) and where the source of primary productivity was clear, the trophic level of consumers was estimated using the following formula:

$$\text{Trophic position}_{\text{consumer}} = (\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}}) / 3.4 + 1 \qquad \textbf{(5.5)}$$

An organism with a trophic position close to 1 is an autotroph / primary producer, 2 is a primary consumer / herbivore, 2.5 is an omnivore consuming plants and primary consumers, 3 is a secondary consumer / predator and 3.5 is an omnivore consuming secondary consumers.

Relative contributions of potential prey to consumers

The average isotope values were calculated for the sources of primary productivity and the proportion of each potential source of primary productivity at the bottom of the food chain was calculated for the fishes and for some of their invertebrate prey. As there were many more sources of primary productivity than isotopes analysed, the ISOSOURCE model was used to calculate the feasible combinations (0-100 %) of the contributions of primary producers to consumers in small increments of 1 % (Phillips and Gregg 2003). Any combination which summed to within 0.01 ‰ of the consumer signature, was considered as a feasible solution. The contributions are reported in terms of the 1^{st} - 99^{th} percentiles rather than the range, as the percentiles are less sensitive to small numbers on the tails of the distribution (Phillips and Gregg 2003). The isotope values of the assumed primary or secondary consumers were corrected for one (3.4 ‰ for $\delta^{15}N$ and 1 ‰ for $\delta^{13}C$) or two (6.8 ‰ for $\delta^{15}N$ and 2 ‰ for $\delta^{13}C$) trophic levels of enrichment respectively, except where stated.

Results

The $\delta^{13}C$ and $\delta^{15}N$ values of the samples from Tollesbury, Abbotts Hall, and Orplands, are presented in Figure 5.1. The sample sizes, C:N ratios and the $\delta^{13}C$ and $\delta^{15}N$ values of the potential sources of primary productivity, the invertebrates and fishes are presented in Tables 5.2, 5.3 and 5.4, respectively.

Primary producers

The sources of primary productivity were isotopically distinct. The $\delta^{13}C$ values of the primary producers exhibited a wide range, from *Spartina*, a C_4 plant, which was the most $\delta^{13}C$ enriched (-14 ‰) to the C_3 saltmarsh plants which were the most ^{13}C depleted (-24 to -27 ‰). These values are characteristic of plants that have the C_4 and C_3 photosynthetic pathways, respectively (Smith and Epstein 1971). The isotope values of the C_3 plants from within and outside Abbotts Hall managed realignment site were not significantly different (ANOVA, $F = 1.36$, $P > 0.05$). The $\delta^{13}C$ values of the other primary producers were intermediate within the range of the vascular plants. The mean $\delta^{13}C$ values for microphytobenthos (MPB) and *Ulva* spp. were -18 to -20 ‰, and -19 to -16 ‰, respectively.

The $\delta^{15}N$ values for the primary producers had a smaller range (6.5 to 12.5 ‰) than the $\delta^{13}C$. There was a significant difference between the $\delta^{15}N$ values of the primary producers within Tollesbury and within Abbotts Hall managed realignment sites (ANOVA, $F = 3.73$, $P < 0.05$ and $F = 33.42$, $P < 0.001$, respectively), in both cases because the microphytobenthos were significantly ^{15}N depleted relative to the other primary producers (Tukey's test, critical value = 4.27 and 4.83, respectively). Data for the microphytobenthos at Orplands were anomalously ^{13}C enriched and were not included in the analysis. The nitrogen isotope values of the primary producers from

Tollesbury were slightly lower than at Abbotts Hall and Orplands managed realignment sites, but these differences were not significant (ANOVA, $F = 2.28$, $P > 0.05$). There was no difference between the isotope values of the primary producers within and outside the Abbotts Hall managed realignment area in the established marsh.

Detritus

The small (55-250 μm) POM samples were dominated by detritus and benthic diatoms (mainly *Pleurosigma* spp.) with lesser amounts of phytoplankton (mainly *Bellerochea* spp. and *Thalassiosira* spp.). The large (250-500 μm) POM sub-samples, caught in a zooplankton net, were dominated by detritus, but also contained benthic harpacticoid copepods (mainly *Tisbe furcata* and *Enterpina* spp.), and calanoid copepods (mainly *Calanus* spp. and *Acartia* spp.).

The $\delta^{13}C$ values of the small suspended POM fraction (-19 and -21 ‰) were similar to previously quoted phytoplankton values (Boutton 1991; Fry 1996) but the isotope values were similar to large POM at Tollesbury and Abbotts Hall, because they were dominated by detritus and microphytobenthos which generally have lower $\delta^{13}C$ values (-18 to -20 ‰) than living phytoplankton. The $\delta^{13}C$ values of large POM at Orplands were extremely ^{13}C depleted and ^{15}N enriched so they were not included in these analyses. Further evidence that the small POM was dominated by detritus at Tollesbury and Orplands, was that the $\delta^{13}C$ and $\delta^{15}N$ isotope values of the POM were similar to the isotope values of the SOM and the C:N ratios were similarly low. At Abbotts Hall, the POM subsamples were also dominated by detritus and MPB but also contained a mixture of nematodes, harpacticoid copepods and some phytoplankton, which was reflected in the higher $\delta^{13}C$ and $\delta^{15}N$ isotope values compared to the POM from the other sites. In addition, at Abbotts Hall, the C:N ratios and $\delta^{13}C$ and $\delta^{15}N$ isotope values of the SOM were more depleted than the values from Tollesbury and Orplands sites.

The isotope values of the strandline detritus samples from Tollesbury and Abbotts Hall were close to those of the C_3 plants, with some depletion in ^{15}N and some enrichment in ^{13}C. The depletion in ^{15}N is characteristic of plant material undergoing some fungal or epiphytic organism breakdown (Currin et al. 1995). At Orplands the isotope values of the strandline detritus were more similar to the SOM than to the C_3 plants suggesting that the strandline material was more broken down than at the other two sites. Although these samples were collected from the strandline, the C_3 detritus would be expected to be present throughout the system.

Figure 5.1A: Plot of $\delta^{13}C$ and $\delta^{15}N$ values (‰ ± 1SD) from Tollesbury managed realignment. Primary producers (□, shaded ovals): *Ulva*= *Ulva* spp, MPB= microphytobenthos, m= managed realignment. Invertebrates (▲): CC= Calanoid copepods, Cm= *Carcinus maenas*, G= Gammarid, H= *Hydrobia ulvae*, HC= Harpacticoid copepods, I= *Idotea linearis*, N= *Nereis diversicolor*, P= *Pleurobranchia pileus*, Pa= *Palaemonetes varians*, S= *Sepia officinalis*. Fishes: ○= *Dicentrarchus labrax*, ●= *Atherina presbyter*, ●= *Pomatoschistus microps*, ●=*Liza ramada*, ●=*Sprattus sprattus*

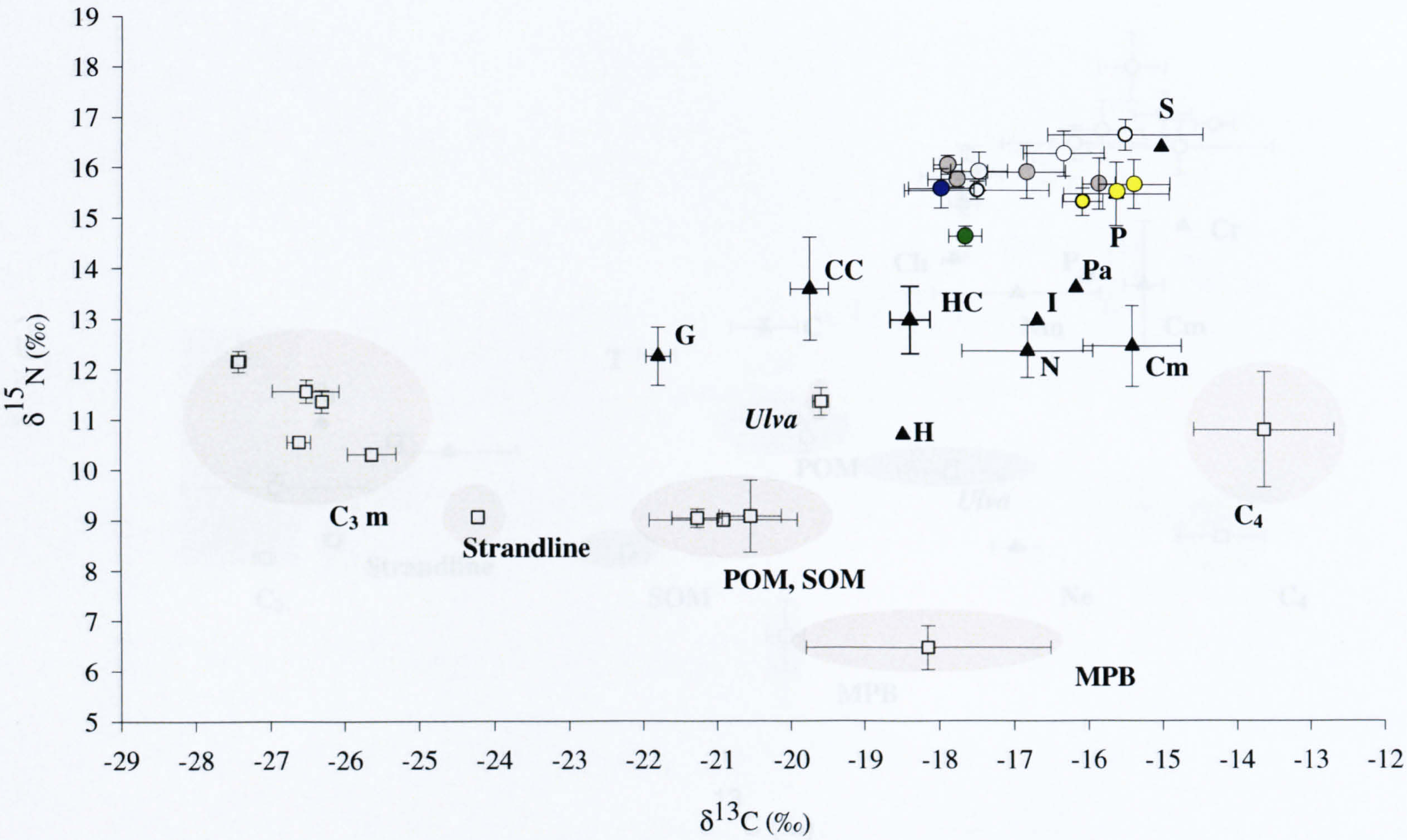


Figure 5.1B: Plot of $\delta^{13}C$ and $\delta^{15}N$ values (‰ ± 1SD) from Abbotts Hall managed realignment site. Primary producers (□, shaded ovals): *Ulva* = *Ulva* spp., MPB= Microphytobenthos. Invertebrates (▲): C= Calanoid and harpacticoid copepods, Ch= Chironomid, Cm= *Carcinus maenas*, Cr= *Crangon crangon*, N= *Nereis diversicolor* m= managed realignment area, e= established marsh, P= *Pleurobranchia pileus*, Pa= *Palaemonetes varians*, S= *Sepia officinalis*, T= Talitrid, Th= Thysanoptera. Fishes: ○=*Dicentrarchus labrax*, ●=*Atherina presbyter*, ○=*Pomatoschistus microps*

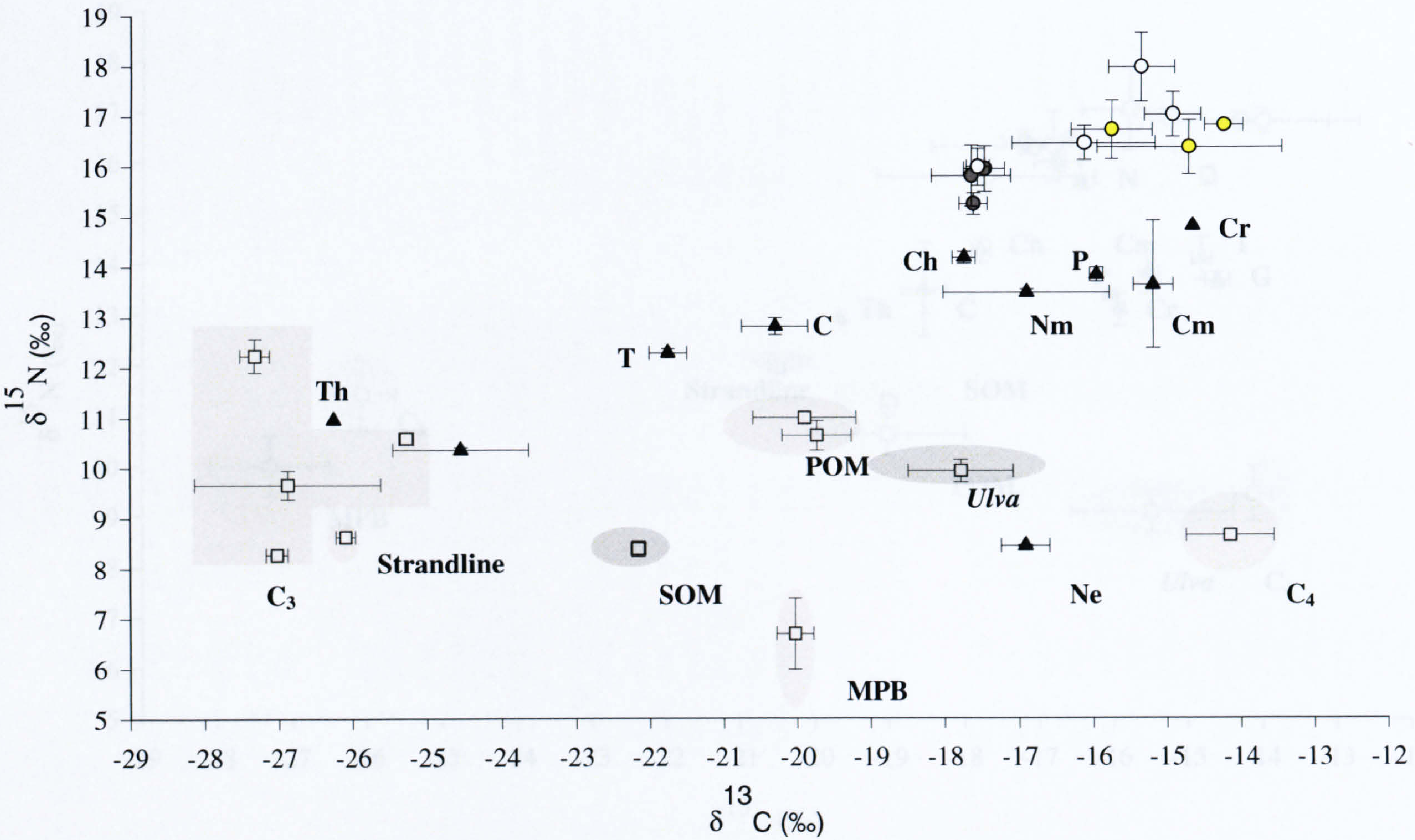


Figure 5.1C: Plot of $\delta^{13}C$ and $\delta^{15}N$ values (‰ ± 1SD) from Orplands managed realignment site. Primary producers (□, shaded ovals): *Ulva*= *Ulva* spp. Invertebrates (▲): C= Calanoid and harpacticoid copepods, Ch = Chironomid, Cm= *Carcinus maenas*, Cr= *Crangon crangon*, G= Gammarid, I= *Idotea linearis*, N = *Nereis diversicolor*, e= established marsh, P= *Pleurobranchia pileus*, Pa= *Palaemonetes varians*, Th= Thysanoptera. Fishes: ○= *Dicentrarchus labrax*, ● = *Atherina presbyter*, ○= *Pomatoschistus microps*

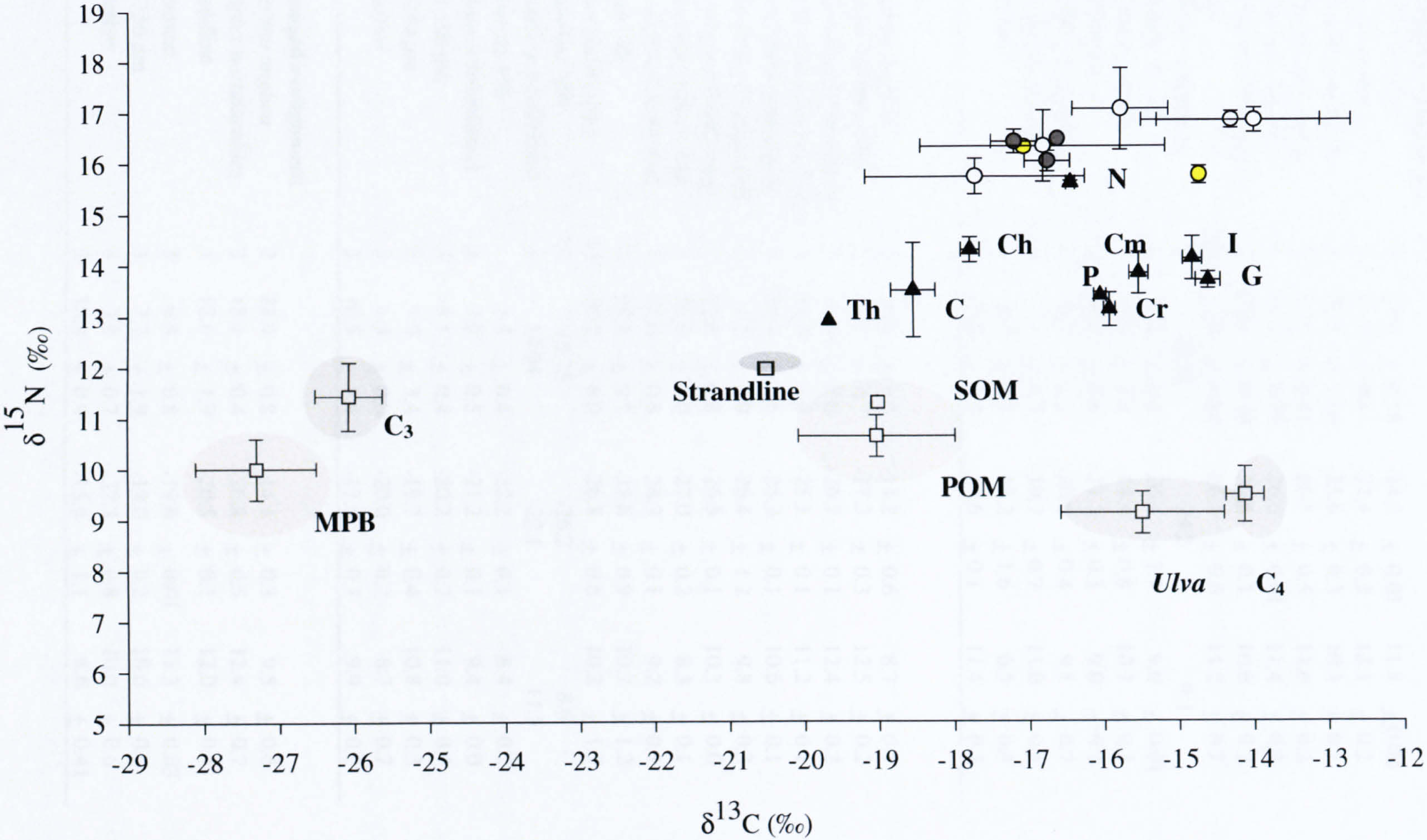


Table 5.1: The C: N ratios, $\delta^{13}C$, and $\delta^{15}N$ (‰ ± 1 SD) of basal resources from the three managed realignments, 'MR' and 'Established' saltmarsh adjacent to Abbotts Hall (summer 2007)

Sample details		n	C:N		$\delta^{13}C$		$\delta^{15}N$	
Tollesbury managed realignment								
C_4	*Spartina anglica*	3	19.8	± 0.18	-14.2	± 0.01	11.4	±0.02
C_3	*Suaeda maritima*	2	13.9	± 0.4	-27.4	± 0.1	12.1	± 0.2
	Puccinellia maritima	2	25.3	± 1.16	-25.6	± 0.3	10.3	± 0.1
	Salicornia europaea	2	12.5	± 0.41	-26.5	± 0.5	11.6	± 0.2
	Limonium vulgaris	2	17.6	± 0.73	-26.3	± 0.01	11.4	± 0.2
	Atriplex portulacoides	2	17.8	± 0.38	-26.6	± 0.1	10.6	± 0.2
	Mean	10	17.4	± 4.94	-26.5	± 0.6	11.2	± 0.7
	Detritus – strandline	1	21.34		-24.2		9.1	
SOM	Sediment Jul-07	2	7.4	± 0.4	-20.4	± 1.7	9.0	± 0.01
	Sediment Aug-06	2	9.4	± 2.3	-18.4	± 0.8	10.2	± 0.3
POM	250-500 µm	3	9.2	± 0.8	-21.3	± 0.3	9.0	± 0.2
	55-250 µm Jul-07	3	6.7	± 1.2	-20.6	± 0.4	9.1	± 0.7
	55-250 µm Aug-06	3	7.1	± 0.7	-19.7	± 0.7	11.0	± 0.4
Microphytobenthos		3	8.7	± 0.3	-18.2	± 1.6	6.5	± 0.4
Ulva spp.		3	17.8	± 2.5	-19.6	± 0.1	11.4	± 0.3
Abbotts Hall								
C_4	*Spartina anglica*	3	21.9	± 1.3	-14.2	± 0.6	8.7	± 0.1
C_3	*Suaeda maritima* MR	2	13.7	± 0.7	-27.3	± 0.3	12.5	± 0.2
	S. maritima Established	2	11.9	± 0.0	-26.7	± 0.1	12.4	± 0.2
	Puccinellia maritima MR	3	31.7	± 1.6	-25.1	± 0.1	11.2	± 0.1
	P. maritima Established	3	14.9	± 1.5	-25.3	± 0.1	10.6	± 0.1
	Salicornia europaea MR	3	9.3	± 1.0	-26.4	± 1.2	9.8	± 0.3
	S. europaea Established	3	12.8	± 0.8	-26.3	± 0.1	10.3	± 0.0
	Limonium vulgaris MR	3	19.6	± 1.0	-27.0	± 0.2	8.3	± 0.1
	L. vulgaris Established	3	25.0	± 0.6	-24.3	± 0.1	9.2	± 0.1
	Mean MR	11	18.6	± 9.7	-25.6	± 0.9	10.7	± 1.2
	Mean Established	11	16.2	± 6.0	-26.8	± 0.6	10.2	± 1.7
Detritus	Strandline MR	1	18.75		-26.2		8.6	
	Strandline Established	1	14.94		-22.1		11.5	
SOM	Sediment MR		3.4	± 0.4	-22.2	± 0.1	8.4	± 0.2
	Sediment Established	3	7.2	± 0.5	-21.2	± 0.1	9.4	± 0.0
POM	250-500 µm	3	4.1	± 0.4	-20.2	± 0.2	11.0	± 0.1
POM	55-250 µm	3	7.0	± 3.4	-19.7	± 0.4	10.8	± 0.3
Microphytobenthos		3	4.3	± 0.0	-20.0	± 0.2	6.7	± 0.7
Ulva spp.		2	10.5	± 1.4	-17.8	± 0.7	9.9	± 0.2
Orplands managed realignment								
C_4	*Spartina anglica*	2	21.4	± 0.8	-14.1	± 0.3	9.5	± 0.6
C_3	*Atriplex portulacoides*	3	18.1	± 0.4	-26.8	± 0.5	12.4	± 0.7
Detritus	Strandline	3	12.6	± 1.9	-20.5	± 0.1	12.0	± 0.1
SOM	Sediment	3	9.8	± 0.8	-19.0	± 0.01	11.3	± 0.03
POM	55-250 µm	3	7.7	± 1.9	-19.0	± 0.2	10.6	± 0.6
Microphytobenthos		3	3.3	± 0.7	-27.3	± 0.8	10.0	± 0.6
Ulva spp.		2	10.9	± 0.9	-15.6	± 1.1	8.6	± 0.41

Invertebrates

The relative contributions of the primary producers to the diets of the primary consumers could be ascertained using the isotopes of carbon and nitrogen, because the baseline isotope values were distinct and occupied a plane in 2 dimensional isotopic space, rather than a straight line (Fry and Sherr 1984; Wainright et al. 2000). The range of invertebrate $\delta^{13}C$ values was within the range of the primary producers. The C:N ratios of each group of invertebrates were similar between the sites (Table 5.1). The sources of primary productivity that some of the invertebrates depend on, was identified by the use of ISOSOURCE as described below.

Tollesbury

At Tollesbury, the gammarid amphipods were the most ^{13}C depleted of the invertebrates sampled. The C_3 detritus collected from the strandline ranked highest in its potential dietary contribution (65-79 %), the POM/SOM ranked intermediate (0-28 %) and the potential contributions of microphytobenthos was small (0-16 %).

The calanoid copepods were more ^{13}C enriched than the gammarids but were more ^{13}C depleted than the other invertebrates. The POM/SOM ranked high in its feasible contribution (0-33 %) to the diets along with C_3 detritus collected from the strandline (16-50 %), as resuspended detritus is the most likely food source for these pelagic zooplankters. Alternative contributions included *Ulva* spp. spores (26-58 %) and C_4 in particulate detrital form (0-21 %).

The harpacticoid copepod samples were more ^{13}C enriched and ^{15}N depleted than the calanoid copepod samples. The POM / SOM and *Ulva* spp. spores ranked highly in the feasible contributions to their diets (0-72 % and 0-54 %, respectively). Alternative contributions which were intermediate in their ranking included small particles of C_3 detritus collected from the strandline (0-41 %), resuspended microphytobenthos (0-33 %) and C_4 in particulate detrital form (0-34 %).

The $\delta^{15}N$ values of *Hydrobia ulvae* were lower relative to all the other invertebrates, as microphytobenthos was identified as the most likely food source (69-74 %). The feasible contribution of C_3 detritus was intermediate (15-23 %) and the other sources are likely to have contributed little to its diet (all <17 %).

In the diets of *Idotea linearis* the feasible contributions of POM/SOM and *Ulva* spp. ranked highly (0-40 % and 0-31 %, respectively) as did C_4 plants, and microphytobenthos (29-48 %, and 15-34 %, respectively), whereas the feasible contributions from the C_3 detritus were lower (0-23 %).

In the diets of *Nereis diversicolor*, the microphytobenthos ranked highly as a potential contributor (32-47 %). The possible contributions from POM, *Ulva* spp., and C_4 were intermediate (0-34 %, 0-27 % and 22-39 %, respectively) and lower for the C_3 detritus strandline (0-19 %). After corrections for two trophic levels of enrichment (6.8 ‰ for $\delta^{15}N$ and 2 ‰ for $\delta^{13}C$) in the diets of *Palaemonetes varians,* the microphytobenthos ranked very highly (92-93 %) as the source of primary productivity, and the feasible contributions from the other living and detrital samples were low.

The $\delta^{15}N$ values of the predatory *Sepia officinalis* and *Pleurobrachia pileus* were high. After correction for two trophic levels the contribution of microphytobenthos to the diets for *Sepia officinalis* and *Pleurobrachia pileus* ranked highest (23-35 % and 43-54 %, respectively). The feasible contributions from POM, *Ulva* spp., and C_4 plants to *S.*

officinalis and *P. pileus* were ranked intermediate (0-26 %, 0-19 % and 41-53 % for *S. officinalis* and 0-25 %, 0-20 %, 24-35 % for *P. pileus*, respectively). *Pleurobrachia pileus* consumed small *C. crangon* individuals (personal observation).

Abbotts Hall

At Abbotts Hall, the $\delta^{13}C$ value of the terrestrial insects (Thysanoptera) was the lowest of the invertebrates sampled. The fractionation between Thysanoptera (11 ‰) and potential C_3 plant food sources (8.3 - 12.5 ‰) was less than the 3.4 ‰ $\delta^{15}N$ per trophic level so the mixing model could not be applied. However, their location on the biplot indicates that the diet of the Thysanoptera is predominantly from C_3 plants. The $\delta^{15}N$ and $\delta^{13}C$ values of the talitrid amphipods were consistent with high contributions from the C_3 strandline detritus (48-65 %), in combination with *Ulva* spp. (22-34 %). The feasible contributions to the diets of these talitrids from SOM was intermediate (0-21 %) and of microphytobenthos and C_4 were small (0-7 % and 0-13 % respectively).

The location of the $\delta^{15}N$ and $\delta^{13}C$ values of the copepods and chironomids was consistent with the prediction that POM / SOM detritus was the source of primary productivity (9 ‰ $\delta^{15}N$ and 21 ‰ $\delta^{13}C$). However, the POM from Abbotts Hall contained meiofauna at the second trophic level and therefore was not used in these analyses. Further, it was not possible to determine the sources of primary productivity for the *Palaemonetes varians* from these data.

Although ISOSOURCE could not compute the contributions to the mean $\delta^{15}N$ and $\delta^{13}C$ values of *N. diversicolor* from the managed realignment (Nm), the values within the standard deviation indicate a diet dominated by *Enteromorpha* spp. The markedly low $\delta^{15}N$ values of *N. diversicolor* from the established saltmarsh (Ne) prevented the use of the mixing model however, the location on the biplot indicates that the microphytobenthos was the most likely source of primary productivity.

In the diets of *C. crangon*, the C_4 plants and microphytobenthos ranked highly in their contribution (34-53 and 32-45 %, respectively) whereas possible contributions from *Ulva* spp. (0-18 %), SOM (0-19 %), and C_3 detritus (0-12 %) were small.

Orplands

As the microphytobenthos isotope values from Orplands were anomalous (see above), it was not possible to determine quantitatively the potential sources of primary productivity. However some trends were evident. The location of the $\delta^{15}N$ and $\delta^{13}C$ values of the chironomids and copepods on the plot were consistent with a diet of POM, as at the other sites. Also *P. varians* occupied a similar position on the graph to those from Tollesbury.

At all three sites, the isotope values of *Carcinus maenas* were the result of complex trophic relationships relating to a scavenging, cannibalistic and herbivorous diet. It was not possible to estimate the contributions of potential food sources using the mixing model. However, the locations of the crabs on the graphs are consistent with the possibility that microphytobenthos and *Ulva* spp. are important sources of primary productivity.

Table 5.2: The C:N ratios, $\delta^{13}C$, $\delta^{15}N$ (‰ ± 1 SD) and trophic level 'TL' of invertebrates from the three managed realignment sites 'MR' and 'Established' saltmarsh adjacent to Abbotts Hall (summer 2007)

Sample details	n	C:N	$\delta^{13}C$	$\delta^{15}N$	TL
Tollesbury managed realignment					
Talitridae	2	5.3 ± 0.0	-21.8 ± 0.2	12.3 ± 0.6	2
Calanoida & Harpacticoida	2	5.3 ± 0.5	-19.8 ± 0.3	13.6 ± 1.0	2.5
Harpacticoida	3	5.7 ± 1.2	-18.4 ± 0.3	12.9 ± 0.7	2
Hydrobia ulvae	1	2.3	-18.5	10.7	2
Idotea linearis	1	4.9	-16.7	13.0	2
Nereis diversicolor	2	4.2 ± 0.1	-16.8 ± 0.9	12.4 ± 0.5	3
Palaemonetes varians	3	3.7 ± 0.3	-16.2	13.6	3
Carcinus maenas	3	4.9 ± 0.1	-15.4 ± 0.7	12.5 ± 0.8	3
Pleurobrachia pileus	1	4.0 ± 0.2	-15.6	15.5	4
Sepia officinalis	1	3.7	-15.0	16.4	4
Abbotts Hall managed realignment and established saltmarsh					
Talitridae MR	2	5.1 ± 0.1	-21.8 ± 0.3	12.3 ± 0.1	2
Talitridae Established	2	5.6 ± 0.2	-20.5 ± 0.3	12.4 + 0.0	-
Calanoida & Harpacticoida	6	5.6 ± 0.4	-20.3 ± 0.5	12.8 ± 0.2	2
Diptera- Chironomidae	4	4.7 ± 0.1	-17.7 ± 0.2	14.2 ± 0.1	3
Idotea linearis	2	4.9 ± 0.5	-24.5 ± 0.9	10.4 ± 0.1	2
Nereis diversicolor MR	3	4.1 ± 0.0	-16.9 ± 1.1	13.5 ± 1.1	3
N. diversicolor Established	3	4.5 ± 0.0	-16.9 ± 0.3	8.4 ± 0.1	2
Palaemonetes varians	3	3.3 ± 0.9	-15.9 ± 0.1	13.9 ± 0.1	3
Crangon crangon	1	3.7	-14.7	14.8	3
Carcinus maenas MR	2	4.8 ± 0.6	-15.2 ± 0.1	13.7 ± 1.3	3
Carcinus maenas Established	2	4.3 ± 0.5	-15.2 ± 0.3	13.3 ± 1.6	3
Thysanoptera	1	5.2	-26.3	11.0	2
Orplands managed realignment					
Calanoid and Harpacticoida	3	5.5 ± 0.2	-18.5 ± 0.3	13.5 ± 0.5	-
Diptera- chironomidae	3	5.6 ± 0.0	-17.8 ± 0.1	14.3 ± 0.3	-
Idotea linearis	3	5.0 ± 0.2	-14.8 ± 0.1	14.1 ± 0.4	-
Gammaridae	3	5.0 ± 0.1	-14.6 ± 0.2	13.7 ± 0.2	-
Nereis diversicolor	3	5.5 ± 0.1	-16.5 ± 0.1	15.6 ± 0.04	-
Palaemonetes varians	3	3.0 ± 0.5	-16.1 ± 0.1	13.4 ± 0.1	-
Crangon crangon	3	4.7 ± 0.1	-15.9 ± 0.1	13.1 ± 0.3	-
Carcinus maenas	3	4.6 ± 0.1	-15.5 ± 0.1	13.8 ± 0.4	-
Thysanoptera	1	10.5	-19.7	12.9	2

Fishes

The $\delta^{13}C$ values for fishes varied over a smaller range (-18 to -14 ‰) than the invertebrates and sources of productivity (see above). The $\delta^{15}N$ values of the fishes ranged from 14.1‰ in small *Liza ramada* to 18 ‰ in small 1-group *Dicentrarchus labrax*. There were no significant differences in the C:N ratios and the $\delta^{13}C$ and $\delta^{15}N$ values of fishes in the different size groups between the three sites therefore the data from the three sites were pooled (Table 5.2 and Figure 5.2). There were significant differences between the $\delta^{13}C$ values (ANOVA, $F = 18.05$, $P < 0.001$) and the $\delta^{15}N$ values (ANOVA, $F = 10.07$, $P < 0.001$) of all the species. The $\delta^{13}C$ values of the zooplanktivorous fishes (small *D. labrax*, *Sprattus sprattus*, and *Atherina presbyter*) were low compared with *Pomatoschistus microps* and large *D. labrax*.

Dicentrarchus labrax

There was a significant difference between the $\delta^{13}C$ values of the different length classes of *D. labrax* (ANOVA, $F = 24.96$, $P < 0.001$) which showed progressive ^{13}C enrichment with size up to 60 mm (Table 5.3, Figure 5.2). The smallest (20-29 mm) individuals were significantly more ^{13}C depleted than the other size classes. The 70-79 mm and 90-120 mm sized *D. labrax* that were 1-group fish did not continue this ^{13}C enrichment progression. There was also a significant difference between the ^{15}N values of different sizes of *D. labrax* (ANOVA, $F = 17.43$, $P < 0.001$).

With increased bass size there was a reduction in the feasible contributions to their sources of primary productivity from the POM (from a maximum of 67 % in 20-29 mm individuals to 41 % in 90-120 mm individuals) and the C_3 detritus (from a maximum of 38 % in 20-29 mm individuals down to 22 % in 90-120 mm individuals respectively). This coincided with the ontogenetic dietary shift from zooplankton to benthic macroinvertebrates. With increasing fish length, the feasible contributions to the sources of primary productivity from *Ulva* spp. and microphytobenthos remained relatively high (between 0-42 % and 13-39 %, respectively in 20-29 mm individuals, and between 0-33 % and 11-30 %, respectively in 90-120 mm individuals).

Atherina presbyter

The $\delta^{13}C$ values of the *Atherina presbyter* individuals in the largest size class were significantly heavier compared with the three smaller size classes (ANOVA, F = 25.92, P < 0.001) (Table 5.3, Figure 5.2). There was no significant difference in the $\delta^{15}N$ values of the different sized *A. presbyter*. As *A. presbyter* increased in size (from 30-39 mm, 40-49 mm, 50-59 mm and 80-89 mm) there was a gradual shift in the diet from zooplankton to benthic meiofauna (Figure 5.4). This corresponded to a decline in the relative contributions to the sources of primary productivity from POM (from a maximum of 76 % in 30-39 mm individuals down to 18 % in 80-99 mm individuals) and C_3 detritus (from a maximum of 44 % down to 0 % respectively). With increasing fish size, there was also a gradual increase in the possible contribution of microphytobenthos (from 0-34 % in 30-39 mm individuals up to 42-51 % in 80-99 mm individuals) and C_4 plants (from a maximum of 28 % in 30-39 mm individuals up to between 33 and 43 % in 80-99 mm individuals).

Pomatoschistus microps

The $\delta^{13}C$ or $\delta^{15}N$ values for *P. microps* in the three size classes were not significantly different. The gut contents analysis revealed no shift in diet, with a dominance of benthic meiofauna in all three size classes (Table 5.3, Figure 5.2). The locations of the $\delta^{13}C$ and $\delta^{15}N$ values of *P. microps* between 20-29mm and 40-49 mm on the plot, were consistent with a mixture of detritus POM / SOM (a maximum of 20-29 %, respectively) and microphytobenthos (a maximum of 40-57 %, respectively) as the sources of primary productivity. The maximum feasible contributions from C_4 plants were intermediate (13-29 % in 20-29mm individuals and 28-41 % in 40-49mm individuals, respectively). The maximum contributions to the sources of primary productivity from C_3 detritus and *Ulva* spp. were low (maximums less than 22 %).

Liza ramada

The $\delta^{15}N$ values of *Liza ramada* (20-39 mm) were lighter than similarly sized *D. labrax*, *P. microps* and *S. sprattus* and confirmed the gut content analysis that indicated that these individuals were omnivorous, feeding on harpacticoid copepods and microphytobenthos predominantly (Table 5.3, Figure 5.2). After correction for 1.5 trophic levels (-1.5 ‰ for $\delta^{13}C$ and -5.1 ‰ for $\delta^{15}N$), the suspended and sedimented detritus (POM / SOM), C_4 plants, microphytobenthos and *Ulva* spp. ranked highly in terms of feasible contributions to the sources of primary productivity (0-54 %, 13-40 %, 11-37 % and 0-45 %, respectively). The feasible contribution of C_3 detritus collected from the strandline was relatively low (and 0-28 %, respectively).

Sprattus sprattus

The $\delta^{13}C$ and $\delta^{15}N$ values of *Sprattus sprattus* (30-49 mm) placed them within the group of other zooplanktivorous fish. This finding was consistent with the gut contents analysis which showed a diet of zooplankton only (Table 5.3, Figure 5.2). Organic detritus (POM / SOM) ranked highly in terms of feasible contributions to the sources of primary productivity (0-76 %) via their diet of copepods mostly. Feasible contributions from microphytobenthos (15-41 %), *Ulva* spp. (0-30 %), C_3 detritus (0-42 %), C_4 (13-40 %) were intermediate.

Isotope values of fishes of the same size

There was a significant difference between the ^{13}C values of *P. microps, D. labrax* and *A. presbyter* in the 30-39 mm size class (ANOVA, $F = 25.92$, $P < 0.001$) because the *P. microps* were significantly more enriched than the other two species (Figure 5.2). There was also a significant difference between the $\delta^{13}C$ values of the three species at the 40-49 mm size class (ANOVA, $F = 6.58$, $P < 0.01$) because the *P. microps* were significantly more ^{13}C enriched than the *A. presbyter*.

There were no significant differences between the $\delta^{15}N$ values of different species at the 30-39 mm or 40-49 mm size classes. There was a significant difference between the $\delta^{13}C$ values of the *A. presbyter* and *D. labrax* at the same 50-59 mm size class (ANOVA, $F = 32.80$ $P < 0.01$) because the $\delta^{13}C$ values of *A. presbyter* samples were significantly lighter than the $\delta^{13}C$ values of the *D. labrax* specimens. There was also a significant difference between the $\delta^{15}N$ values (ANOVA, $F = 8.06$, $P < 0.01$) because the $\delta^{15}N$ values of the *D. labrax* samples were more ^{15}N enriched.

Table 5.3: The C:N ratios, $\delta^{13}C$, $\delta^{15}N$ (‰ ± SD) and trophic level 'TL' of fishes from the three managed realignment sites 'MR' and 'Established' saltmarsh adjacent to Abbotts Hall (summer 2007)

Species	Length, mm	n	C:N	$\delta^{13}C$	$\delta^{15}N$	TL
Tollesbury						
Liza ramada July 2007	20-39	3	4.2 ± 0.0	-17.7 ± 0.2	14.6 ± 0.2	2.5
Liza ramada Sept. 2006	20-39	10	3.7 ± 0.3	-17.4 ± 0.8	14.1 ± 0.6	2
Sprattus sprattus	30-49	3	3.8 ± 0.0	-18.0 ± 0.4	15.6 ± 0.4	3
Atherina presbyter	30-39	3	3.6 ± 0.1	-17.9 ± 0.3	16.0 ± 0.1	3
	40-49	3	3.5 ± 0.0	-17.8 ± 0.4	15.8 ± 0.2	3
	50-59	3	3.6 ± 0.1	-17.6 ± 0.1	16.1 ± 0.5	3
	80-99	3	3.4 ± 0.0	-16.1 ± 0.2	15.7 ± 0.5	3
Pomatoschistus microps	20-29	3	3.7 ± 0.1	-16.1 ± 0.3	15.3 ± 0.3	3
	30-39	3	3.7 ± 0.1	-15.6 ± 0.7	15.5 ± 0.6	3
	40-49	3	3.7 ± 0.2	-15.4 ± 0.5	15.7 ± 0.5	3
Dicentrarchus labrax	20-29	5	3.6 ± 0.3	-17.5 ± 0.4	15.9 ± 0.4	3
	30-49	3	3.6 ± 0.4	-17.5 ± 1.0	15.5 ± 0.2	3
	50-69	6	2.3 ± 1.6	-16.3 ± 0.6	16.3 ± 0.4	3
	90-129	3	3.3 ± 0.1	-15.5 ± 1.0	16.6 ± 0.3	3
Abbotts Hall						
Atherina presbyter	30-39	3	3.5 ± 0.1	-17.6 ± 0.2	15.3 ± 0.2	3
	40-49	3	3.5 ± 0.1	-17.5 ± 0.5	16.0 ± 0.3	3
	50-59	3	3.6 ± 0.1	-17.6 ± 0.6	15.8 ± 0.5	3
Pomatoschistus microps	20-29	3	3.6 ± 0.1	-15.8 ± 0.6	16.7 ± 0.6	3
	30-39	3	3.7 ± 0.3	-14.2 ± 0.1	16.8 ± 0.3	3
	40-49	3	3.7 ± 0.1	-14.7 ± 0.5	16.4 ± 1.3	3
Dicentrarchus labrax	20-29	3	3.6 ± 0.1	-17.6 ± 0.2	16.0 ± 0.4	3
	30-49	5	3.6 ± 0.1	-16.1 ± 1.0	16.5 ± 0.3	3
	50-69	7	3.4 ± 0.1	-14.9 ± 0.4	17.0 ± 0.4	3.5
	90-129	3	2.4 ± 1.8	-15.4 ± 0.5	18.0 ± 0.5	3.5
Orplands						
Atherina presbyter	40-49	3	3.6 ± 0.0	-16.8 ± 0.2	16.0 ± 0.3	3
	50-59	2	3.6 ± 0.0	-17.2 ± 0.3	16.4 ± 0.4	3
	80-99	1	3.5	-16.6	16.5	3
Pomatoschistus microps	30-39	3	3.6 ± 0.03	-14.7 ± 0.1	15.8 ± 0.2	2.5
	40-49	1	3.6	-17.1	16.3	3
Dicentrarchus labrax	20-29	4	2.4 ± 1.6	-17.7 ± 1.5	15.7 ± 0.3	2.5
	30-49	6	3.6 ± 0.3	-16.8 ± 1.6	16.3 ± 0.7	3
	50-69	7	3.4 ± 0.2	-14.3 ± 1.2	16.8 ± 0.2	3
	70-89	4	3.8	-15.8 ± 0.6	15.8 ± 0.6	3
	90-129	2	3.3 ± 0.0	-14.0 ± 1.3	16.8 ± 0.2	3

Figure 5.2: Plot of $\delta^{13}C$ and $\delta^{15}N$ values of juvenile fishes from the Blackwater saltmarshes (mean ‰ $\pm$ 1 SD). ○ = *Dicentrarchus labrax*, ● = *Atherina presbyter*, ● = *Pomatoschistus microps* of different length classes (cm) and ● = *Liza ramada*, ● = *Sprattus sprattus*

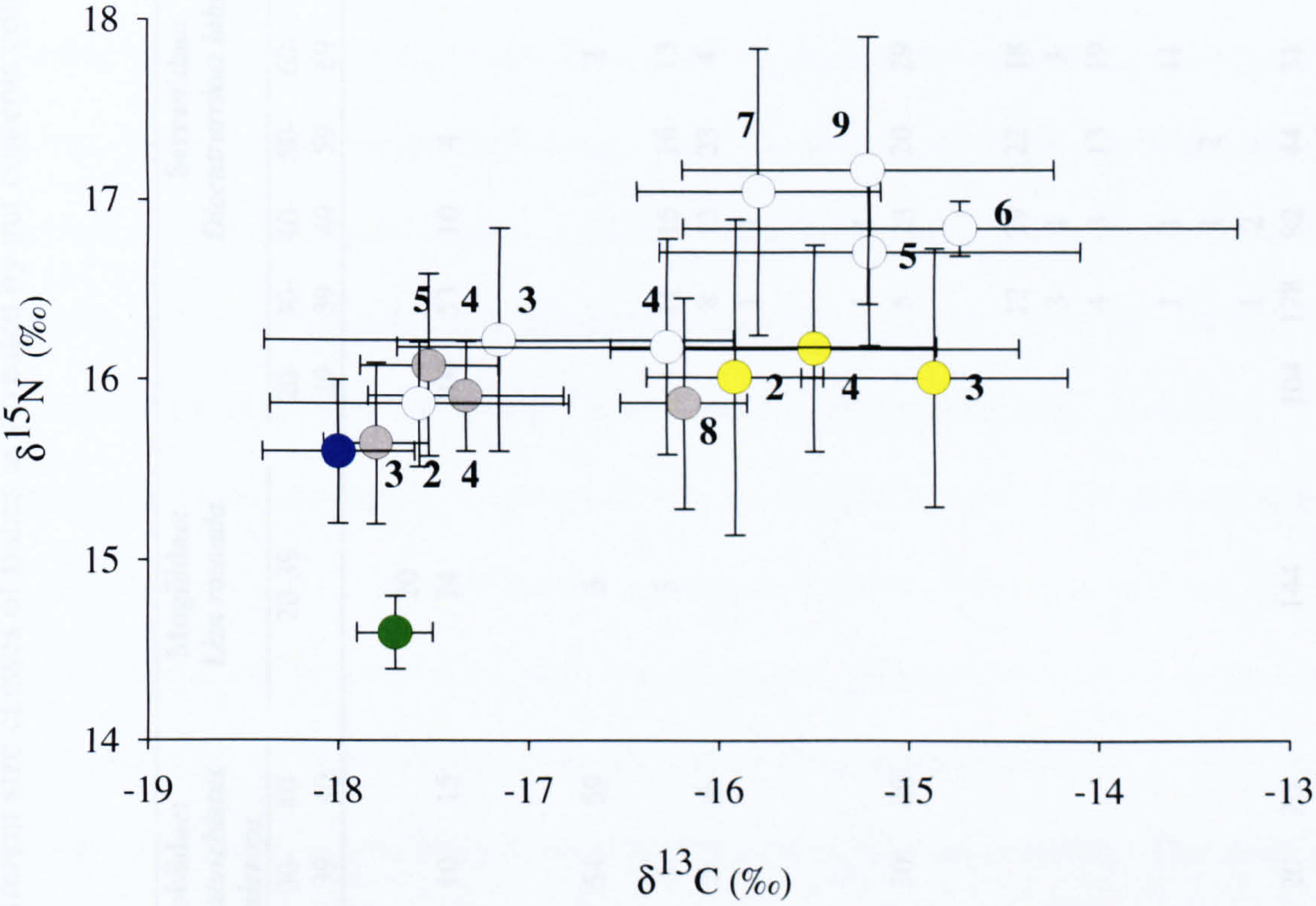


Table 5.4: The prey types (percentage biomass) in the diets of different size classes of fishes as revealed by gut contents collected from the Blackwater Estuary (2005 and 2007)

Species	**Atherinidae:** *Atherina presbyter*				**Clupeidae:** *Sprattus Sprattus*	**Gobiidae:** *Pomatoschistus microps*			**Mugilidae:** *Liza ramada*	**Serranidae:** *Dicentrarchus labrax*							
Length (mm)	30-39	40-49	50-59	80-99	30-49	20-29	30-39	40-49	20-39	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-129
Prey																	
Benthic diatoms									20								
Zooplankton	100	87	56		100	6	10	15	74	100	53	10	4			9	
Benthic meiofauna (megalopa, halicarida, ostracoda harpacticoida)		13		10		87	54	59	3					2			
Terrestrial invertebrates			31	4		7	1		3		11	15	16	13	4		
Nereis diversicolor							5	6			8	13	23	4	14	10	28
Diptera larvae											1	1					
Epibenthic macrofauna																	
Hydrobia ulvae			13	86							1	1					
Carcinus maenas							30	20			5	23	20	29	67	25	34
Hyperbenthic macrofauna																	
Amphipoda											12	29	22	18	12	12	12
Isopoda											3	1		3		2	3
Crangon crangon											4	3	13	19	4	11	18
Palaemonetes varians											1	1		11		26	2
Neomysis integer												1	2			2	3
Fish											1	2				3	
N	5	5	5	5	45	20	20	20	144	104	178	82	44	31	10	22	45
Date	July-August 2007				March 2006	July-August 2007			October 2006 – January 2007	July-September 2005-2006							

Discussion

The results from this study demonstrate the complex nature of saltmarsh food webs and the importance of a number of sources of primary productivity, including detritus, MPB, and to a lesser extent C_3 plants and *Enteromorpha* spp. The stable isotope analyses revealed three interlinked pathways. Firstly, ^{13}C depleted POM containing resuspended detritus, bacteria and microphytobenthos, was the source of primary productivity to zooplankton and consequently small (<50 mm) zooplanktivorous fishes such as *Sprattus sprattus*, *Dicentrarchus labrax*, and *Atherina presbyter*. Secondly, fresh and detrital ^{13}C depleted C_3 vegetation and *Ulva* spp. fronds were the source of primary productivity for some herbivorous amphipods, isopods and insects, and contributed to the diets of larger *D. labrax*. Thirdly ^{13}C enriched benthic microphytobenthos, *Ulva* spp. and detritus in the creeks and the soft sediment were the sources of primary productivity to benthic meiofauna such as harpacticoid copepods and benthic macrofauna such as *Carcinus maenas, Hydrobia ulvae*, *Nereis diversicolor* and *Crangon crangon*. The smaller benthic invertebrates were consumed by *Pomatoschistus microps* (20-50 mm) and *Atherina presbyter* (80-99 mm), and the larger individuals were consumed by small 1-group *D. labrax* (70-129 mm). In addition, small omnivorous *Liza ramada* relied on a mixture of POM and microphytobenthos, via an omnivorous diet of benthic diatoms and harpacticoid copepods, predominantly. The importance of C_3 plant detritus and microphytobenthos in the saltmarsh is consistent with other estuarine systems (Kwak and Zedler 1997; Wainright et al. 2000; Elliott and Hemmingway 2002; Kang et al. 2003; Galvan et al. 2008; Vinagre et al. 2008).

In general the $\delta^{15}N$ values in the food webs in this study were enriched compared with other estuaries (Table 5.3 and 5.5). This finding is consistent with previous studies from the outer Thames and Blackwater Estuaries in which the authors attributed the high

$\delta^{15}N$ values in macroinvertebrates and fishes to microbial processing of treated sewage (Savage 2005; Leakey et al. 2008). The Blackwater has a largely rural catchment, receiving agricultural fertiliser run-off and point-source sewage inputs from towns including Chelmsford (via the River Blackwater), Maldon, and Tollesbury. The managed realignment areas are situated on land that was previously arable and fertilised with nitrogen which would elevate ^{15}N values.

In the Blackwater estuary, hypernutrification can result in excessive seasonal growth of opportunistic green algae, such as *Ulva* spp., over soft sediments and the results from this study show that *Ulva* spp. may be important in the diets of some macroinvertebrates such as *Nereis diversicolor. Ulva* spp. are able to grow rapidly by utilising nutrients from the water column regardless of sediment quality (Engelsen 2008) and may affect the trophic ecology of the habitat by outcompeting autochthonous primary producers such as benthic diatoms (Hubas and Davoult 2006). The substrates of *Ulva* spp. include, but are not limited to, the mudflats, shallow ponds and scrapes, vegetation, and creeks within the managed realignment areas. The ecological costs of excessive *Ulva* spp. growth include sediment anoxia, and reduced diversity of infauna because some invertebrates such as surface suspension feeders (Troell et al. 2005) and *Corophium volutator* (Raffaelli et al. 1991; Raffaelli 2000) are vulnerable to smothering. Post-larval *Platichthys flesus* and *Pomatoschistus microps* (5-10 mm) can also become trapped in floating *Ulva* spp. mats and die (personal observation).

Primary productivity

The phytoplankton (55-250 μm) samples were comprised mainly of detritus and resuspended benthic diatoms, and not phytoplankton. This was despite the fact that phytoplankton blooms occurred in the spring of 2005, 2006, and 2007 in the Blackwater

Estuary (see Chapter 2) in contrast to that of other turbid, light limited estuaries (Kocum et al. 2002; Kromkamp et al. 2005). The suspended POM consisted of C_3 detritus, some MPB and small amounts of phytoplankton, and was identified as the source of primary productivity for the copepods, and then the small zooplanktivorous fishes of *D. labrax*, *S. sprattus* and *A. presbyter*. The POM samples were collected around high tide when there was the least interaction with the sediment. The habitats are silty, shallow and unstratified, thus resuspension rates of MPB and sedimented organic material are high. Previous authors have shown that in some western European saltmarshes the detritus in the unvegetated creeks contribute more to the suspended POM than the C_3 plants (Hemminga et al. 1992).

The saltmarsh vegetation provides both refugia and food to a number of invertebrates. Fresh and semi-degraded C_3 plants and *Ulva* spp. were identified as a food source of herbivorous and detritivorous gammarid, and talitrid amphipods, isopods (*Idotea* spp.) and insects (Thysanoptera). This finding is consistent with a lagoon in the Northwest Mediterranean, where *Idotea* sp. consumed C_3 plants in June but later reverted to a diet of POM in September (Carlier et al. 2007). These invertebrates were consumed by large 0-group and small 1-group *D. labrax*, but not by the other smaller fishes present in these saltmarshes during summer. The herbivorous macroinvertebrates reside within the vegetation or within the moist C_3 halophyte plant debris of the strandline. The strandline also contained diatoms and fine particles from the sediment surface, washed up on the flooding tide. The isotope values of some other amphipods and isopods collected from Orplands and Tollesbury were closely associated with the *Ulva* spp. where they resided. Amphipods reflect the isotope values of the macroalgal debris within which they reside (Adin and Riera 2003) but the exact dietary preference of these herbivores is influenced by differences in the nutritional value of the food sources at different stages of decay

(Buchsbaum et al. 1991; Adin and Riera 2003). In the Mont Saint-Michel Bay, 70 % of the pioneer zone vegetation associated with low marsh communities was estimated to be transported to the strandline where it was consumed by *Orchestia gamarellus*, an important prey species for juvenile 0-group *D. labrax* (Lefeuvre et al. 2000). The strandline habitat and associated prey becomes increasingly available to fish as the marsh is progressively immersed over the lunar cycle, up to the highest spring tides.

The microphytobenthos, predominantly epipelic diatoms, is a major source of primary productivity in this system, as it is in similar systems elsewhere (Underwood and Krompkamp 1999). These diatoms grow at the sediment-water interface in the creeks and soft sediment areas where they are grazed by benthic invertebrates. Here, the reduced water turbulence results in a relatively thick boundary layer and a limited pool of CO_2, thus microphytobenthos are less isotopically discriminating and the $\delta^{13}C$ values are heavier than those of phytoplankton (Currin et al. 1995; France 1995). The nitrogen uptake in diatoms is rapid, and results in increased C_4 metabolism, which in turn elevates the $\delta^{13}C$ values of the microphytobenthos (Fry and Wainright 1991). The ^{15}N values of microphytobenthos were low compared to those in other systems and the reason for this is unknown (Table 5.5). The ^{15}N depletion of MPB relative to SOM was similar to the 2‰ depletion reported previously in the Scheldt Estuary (Moens et al. 2005). In vegetated sites such as Orplands, MPB densities are likely to be greatest in the creeks where there is less shading (Wainright et al. 2000). However benthic diatoms have low light requirements and are not necessarily affected by the short term presence of *Enteromorpha* spp., because of the reduced sediment mixing under the *Enteromorpha* mats (Troell et al. 2005).

Although *Spartina* was included in the ISOSOURCE modelling, it is unlikely to have contributed greatly to the food webs as it is not an abundant halophyte at any of the sites (Jain 2004; Wolters et al. 2005a and personal observations; Spencer et al. 2008) and the $\delta^{13}C$ of all the consumers was isotopically deplete relative to *Spartina*.

Table 5.5: Examples of published $\delta^{13}C$ and $\delta^{15}N$ values of primary producers. R = Reference (see below), Is. = Island, Est = Estuary

Location		R	SOM		POM		C_3 plants		C_4 plants		*Ulva* spp.		MPB	
			$\delta^{13}C$	$\Delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
-	Review	1			-24 to -19	6 to 9			-14 to -13	2 to 9			-18 to -12	1 to 4
UK	Tay Est	2			-27 to -23	3 to 11								
	Blackwater Est	*	**-20**	**10**	**-20 to -19**	**11**	**-27 to -26**	**11 to 12**	**-15 to -14**	**10**	**-18 to -17**	**9 to 10**	**-20 to -18**	**6 to 7**
Nether-	Scheldt Est	3			-24 to -16	8 to 12			-13 to -12	13 to 19			-17 to -14	7 to 8
lands		4	-25 to -23	8 to 10	-22 to -18	9 to 10								
	Oosterschelde	5	-19	7 to 8	-21	6								
France	Marennes-	6			-23 to -21	4 to 6							-17 to -15	5 to 6
	Oleron Bay	7	-20 to -18	6 to 7	-23 to -22	6 to 7								7
	Roscoff-Aber-	8	-19 to -18	8							-17 to -14	9		
	Bay	9	-16 to -15	8	-18 to -17	5	-26 to -25	4 to 7			-17	7	-17	8 to 9
	Anguillon Bay	10	-21 to -20	6 to 7	-22	4 to 6	-25	9	-14 to -13	4 to 6			-15 to -14	4 to 5
	Mont-Saint-	11					-27 to -24	5 to 9	-12	8			-23 to -15	4 to 8
	Michel Bay	12			-22 to -20	3 to 5	-27 to -25	6 to 5	-14	4			-19 to -17	4 to 6
Portugal	Tagus Est.	13	-21	5 to 7	-26 to -24	3 to 4	-28 to -25	10 to 13	-14	8 to 12			-16	8
S. Korea	Peninsular	14	-20 to -19	10 to 11	-22 to -19	10 to 12	-28 to -25	6 to 9	-16 to -13	13 to 15			-15 to -14	10 to 12
Canada	Nova Scotia	15	-18						-13		-10		-14 to -18	
USA	Washington	16							-27		-11 to -10		-21 to -19	
	Tijuana Est.	17			-21 to -20	10 to 12	-27	9 to 11	-16 to -15	7 to 9	-17 to 20	10 to 14	-18 to -15	3 to 5
	S.California	18					-27 to -23		-15 to -14		-17			
	Louisiana	19			-26	3			-14	6			-20	5
		20	-14 to -13	8 to 10	-23 to -17	3 to 4	-29 to -28	8 to 5	-13	2 to 11	-18 to -19	6		3
	Delaware Bay	21			-23 to 20	8			-14 to -12	8-11			-17	10
	Plum Is.Sound	22	-19	3.1	-22	7					-20.9	6		
Australia	Walpole /Leschenault	23	-20 to -16	4 to 5	-20 to -16	4	-25 to -24	2 to 7					-15	4 to 5

References: 1=Currin *et al.*(1995) 2=Thornton & McManus (1994) * = this study 3=Moens et al. (2005) 4=Middleburg & Nieuwenhuize (1998) 5=Riera et al. (2002) 6=Kang et al. (1999) 7=Riera (1996) 8=Adin & Riera (2003) 9=Riera & Hubas (2003) 10=Riera et al. (1999) 11=Creach et al. (1997) 12=Riera (2007) 13=Vinagre et al. (2008) 14=Kang et al. (2003) 15=Schwinghamer et al. (1983)16=Hentschel et al (1998) 17=Kwak & Zedler (1997) 18=Smith & Epstein (1970) 19=Carman & Fry (2002) 20= Winemiller et al (2007) 21=Wainright et al. (2000) 22=Wainright & Fry (1994) 23=Svensson et al. (2007)

Meiofauna

The results from this study show that detritus and microphytobenthos (predominantly epipelic diatoms), are the food sources for benthic meiofauna, such as harpacticoid copepods. In the Scheldt Estuary, copepods were depleted in ^{13}C and enriched in ^{15}N relative to POM and this was attributed to a preference for either phytoplankton or heterotrophs consuming dissolved organic matter of phytoplanktonic origin, which is generally ^{13}C depleted and ^{15}N enriched relative to POM (De Brabandere 2005). Some zooplankters feed on phytoplankton selectively (Martineau et al. 2004). Calanoid copepods such as *Acartia* consume algae >3 μm, detrital material, allochthonous inputs and microzooplankton such as ciliates and tintinids (White and Roman 1992; Hirst et al. 1999). Benthic meiofauna such as harpacticoid copepods consume MPB and they are also microbial gardeners, consuming their own faecal pellets, and the bacteria associated with diatoms (Smith et al. 1979; Decho and Fleeger 1988; Riera 1996; Riera 2004; DeTroch et al. 2005; Moens et al. 2005). Harpacticoid copepods exhibited a dietary preference for the macroalga *Ulva lactuca* in an Alaskan Bay where it was abundant (Fujiwara and Highsmith 1997). The wide range of isotope values of the meiofauna is caused by high turnover rates and fluctuations in dietary preferences, as described above. Carman and Fry (2002) attributed seasonal shifts in the $\delta^{13}C$ values of meiofaunal nematodes and copepods to a nutritional dependence on algae in summer to detritus in winter and more research is required to determine if this occurs within this system also.

Macroinvertebrates

The finding that microphytobenthos, detrital POM and possibly *Ulva* spp. are the most likely sources of primary productivity for the macroinvertebrates *Palaemonetes varians*, *Crangon crangon*, *Carcinus maenas* and chironomids, is consistent with previous studies (Escaravage and Castel 1990; Riera 2004). In addition to the direct consumption of algae and detritus, *Palaemonetes* spp. consume *Hydrobia ulvae*, cladocerans and copepods (Minello and Zimmerman 1992; Samuels and Mason 1997; 1998; Barnes and de Villiers 2000), and *Nereis diversicolor* (Rainbow et al. 2006). The $\delta^{15}N$ values of *Crangon* spp. from the North Sea (Jennings et al. 2002) were slightly depleted (11.3 ‰ $\pm$ 0.49 SD) compared to the $\delta^{15}N$ values in this study, possibly because of a reduction in the influence of sewage with increasing distance away from the Blackwater Estuary. *Crangon* spp. consumes benthic meiofauna such as ostracods and harpacticoid copepods but may also consume amphipods and polychaetes (Pihl and Rosenberg 1984; Minello and Zimmerman 1992; Chul-Woong et al. 2001). *C. maenas* exhibited a large range in $\delta^{15}N$ values, which is indicative of the large range of food sources of this species, spanning more than one trophic level. The *C. maenas* megalopa and juveniles (3-10 mm carapace width) are omnivorous, carnivorous (Jones et al. 1997; Barnes and de Villiers 2000) and in some instances, cannibalistic (Mosksnes et al. 1998). The diets of the adult chironomids reflect filter feeding on surface detrital POM, as in freshwaters (Finlay et al. 2002), however, not all adult chironomids feed. Therefore these values may also reflect only the values of the larvae, which consume microphytobenthos (Goldfinch and Carman 2000) and the ^{15}N enrichment greater than one trophic level above these sources may be attributed to the metabolic processes during pupation (Doi et al. 2007).

The $\delta^{15}N$ and $\delta^{13}C$ values of *Hydrobia ulvae* indicate that microphytobenthos was the source of primary productivity for this species. This result is consistent with that of previous authors who have shown that *H. ulvae* is a selective deposit feeder, consuming organic detritus, secreted mucus, bacteria films, and microphytobenthos which is considered to be the main source of nutrition for this species (Creach et al. 1997; Haubois et al. 2005).

The wide range of $\delta^{15}N$ values of *Nereis diversicolor* found here is consistent with those in other studies (Barnes and de Villiers 2000; Nithart 2000) and confirms the ability of this organism to opportunistically switch between consumption of microphytobenthos (Smith et al. 1997), filamentous algae (Hughes 1999), filter feeding and more predatory feeding strategies (Costa et al. 2006). *Nereis diversicolor* is an opportunistic and omnivorous species which will feed on the prey of greatest abundance or quality, although the main feeding behaviour involves searching for food at the sediment surface (Nordstrom et al. 2006). Herman *et al.* (2000) reported an 86 % dependence on microphytobenthos and Galvan et al. (2008) reported a high dependence of *Nereis diversicolor* on microphytobenthos in the mudflats, but in saltmarsh creek walls they had a greater dependence on phytoplankton.

The results from this study show that *Sepia officinalis* and *Pleurobrachia pileus* are highly ^{15}N enriched predatory carnivores. The diet of young *Sepia officinalis* was dominated by amphipods, Brachyura including *Liocarcinus arcuatus*, and unidentified Macrura (Blanc et al. 1998). *Pleurobrachia pileus* is a non-selective carnivore, consuming zooplankton, particularly fish eggs and larvae, and crustaceans (in some cases, up to 80 % of the diet of *P. pileus* comprised crustaceans) (Fraser 1970).

Fishes

The results in this study identified individual groups of fish consumers ultimately relying on POM, detrital and fresh C_3 plants, microphytobenthos and *Ulva* spp. as the sources of primary productivity on which they ultimately depend. Previous authors have commented on the benefits of using primary consumers as baseline indicator organisms to reduce the variability and improve the accuracy in the estimation of trophic level (Cabana and Rasmussen 1996; Vander Zanden and Ransmussen 1999; Vander Zanden 2001; Mathews and Mazumder 2005). Unfortunately, it was not possible to employ this technique in this study because of the mixed feeding behaviour of the macroinvertebrates, and the presence of just one, rarely consumed, benthic herbivore (*H. ulvae*).

The $\delta^{13}C$ values and gut contents analysis of small *D. labrax*, *S. sprattus* and *A. presbyter* (< 30-50 mm) showed that these individuals were predominantly zooplankton feeders ultimately relying on POM as their source of primary productivity. This zooplanktivorous diet is consistent with results in the literature for juvenile bass (Kennedy and Fitzmaurice 1972; Ferrari and Chieregato 1981; Laffaille et al. 2001a; Hibino et al. 2006) *S. sprattus* (Maes and Ollevier 2002; Maes et al. 2003; Voss et al. 2003; Mollmann et al. 2004; Guelinckx et al. 2006) and *A. presbyter* (Trabelsi et al. 1994; Pinnegar and Polunin 2000). *A. presbyter* may consume benthic meiofauna when zooplankton is unavailable (Trabelsi et al. 1994).

The results of this study show that *Liza ramada* (20-39 mm long) consumes resuspended benthic meiofauna, microphytobenthos, and some insects. *Liza* spp. are characterised by a wide range of feeding behaviours in estuaries, exploiting the water surface film and bottom mud, either by direct grazing or via plant-detritus food chains

(Boglione et al. 2006). Romer and McLachan (1986) highlighted the ontogenetic dietary shift in juvenile *Liza* spp. from planktonic carnivores as juveniles to grazers of surf diatoms as larger fishes. This change coincides with the development of the pharyngobranchial organ from a planktonic filtering structure to a more complex one designed for detritus filtration (Serventi et al. 1996). Larson and Shanks (1996) showed that juvenile *Liza* spp. feed on detrital marine snow when they are between patches of zooplankton and consequently show reduced weight loss. In the Neretva Estuary, Croatia, juvenile *L. ramada* consumed harpacticoid copepods (39 %), insects (32 %) and cladocerans (12 %) (Bartulovic et al. 2007). Similarly, in NE Spain, juvenile *Liza* spp. consumed cladocerans, calanoid and harpacticoid copepods, larval and adult insects, and some polychaetes (Gisbert et al. 1995). In contrast, in the Elmina tidal lagoon in Ghana, juvenile *Liza* sp. consumed bacteria, diatoms, cyanobacteria, protozoans, detritus and particulate organic matter (Blay 1995). Similarly, in the Balearic Islands, juvenile *Liza ramada* consumed benthic microalgae and filamentous green algae in spring, and dinoflagellates and detritus in autumn (Cardona 2001). In a study of the diets of juvenile *Liza ramada* (>100 mm) in the Mont Saint Michel Bay, diatoms and detritus comprised 93 % of the prey items consumed and the rest of the diet was comprised of copepods and nematodes (Laffaille et al. 2002).

Pomatoschistus microps (20-50 mm) and adult *Atherina presbyter* (80-99 mm) exhibited heavier $\delta^{13}C$ values than the smallest measured size classes of 0-group *S. sprattus*, *D. labrax* and *L. ramada*, indicating that these two species exhibit a similar preference for benthic meiofauna and small macrofauna. These fishes occupied a similar trophic position, despite their differences in size and this phenomenon has been highlighted in previous studies (Layman et al. 2005). Prey types include harpacticoid copepods, meroplankton (larvae of benthic organisms), and juvenile *C. maenas* and *H.*

ulvae, which are more ^{13}C enriched than zooplankters because they rely on microphytobenthos predominantly. The importance of meiofauna in the diets of juvenile marine fishes has been stressed several times (Coull 1990; Antholz et al. 1991; Gregg and Fleeger 1997; Coull 1999). Gee (1989) highlighted the importance of harpacticoid copepods in the diets of juvenile fishes, as they are more active and available to fishes than other benthic meiofauna, and have a high energetic efficiency as prey.

Pomatoschistus microps (20-30 mm) are opportunistic predators which consume zooplanktonic and benthic meiofauna, and later exhibit an ontogenetic shift towards small macrofauna including hyperbenthic and epibenthic mysids, amphipods, isopods, bivalves, molluscs, polychaetes, and insects (Jackson et al. 2002; Hampel and Cattrijsse 2004; Pasquaud et al. 2004; Salgado et al. 2004b; Leitao et al. 2006). The $\delta^{13}C$ values of *Atherina presbyter* in this study were similar to that of *Atherina* sp. (40-50 mm) from a Venice lagoon, where the fish consumed harpacticoids and amphipods predominantly, but the $\delta^{13}C$ and $\delta^{15}N$ values reflected a diet of isopods and mysids, and this difference was attributed to differences in the time to assimilate food items (Vizzini and Mazzola 2005). The $\delta^{13}C$ values of *A. presbyter* in this study were also consistent with benthic feeding *A. presbyter* collected from Corsica, France (Pinnegar and Polunin 2000).

Large 0-group and small 1–group *Dicentrarchus labrax* in this study consumed large benthic macroinvertebrates, which were ultimately reliant on microphytobenthos predominantly, and had significantly heavier $\delta^{15}N$ values compared with the other fishes (See Chapter 4 for more details of 0- and 1-group bass diets). The $\delta^{15}N$ values of 60-70 mm bass were consistent with those from a previous study in the North Sea (Jennings et al. 2001). The tissue turnover rate for age 0+ to 1 *D. labrax* white muscle tissue is approximately 7 months (Sweeting et al. 2005), therefore while the isotope values closely reflect the assimilated prey of the small 0-group fishes (<4 months) they are not as accurate for the older small 1-group *D. labrax* (> 14 months old). *D. labrax* grows faster in summer and slower in winter (see Chapter 3 for details of growth rates) and this may explain the ^{13}C enrichment of small 1-group individuals relative to larger 0-group individuals (Perga and Gerdeaux 2005). Some individuals actively seek out warm water outflows during winter, reducing the seasonal difference in growth rates and isotope values for some but not all individuals, thereby increasing the overall variability between all *D. labrax*, which can fluctuate by as much as $\pm$ 2.74 ‰ SD (Barnes et al. 2007). Further research is required to determine the site fidelity of *D. labrax* to particular saltmarsh habitats at different spatial and temporal scales.

In conclusion, the results from this study have revealed the importance of microphytobenthos, detritus, C_3 plants and *Ulva* spp. as interlinked basal resources to a wide range of invertebrates and fishes, in particular *D. labrax*, in restored saltmarshes in Essex. The value of microphytobenthos both in resuspended form and on the surface of the mud highlights the importance of the soft sediment microhabitats to a wide range of macroinvertebrates and, ultimately, fishes. These soft sediment feeding habitats could include a dendritic creek system with a large surface area for diatom growth which would be inhabited by fishes frequently, as well as shallow ponds, scrapes and salt pans which would also function as refuge areas for reproducing invertebrates. The importance of microphytobenthos to the food chain and ultimately to fish nursery habitats adds strength to the move to reduce the use of herbicides and bioaccumulating chemicals in the hinterland farms and in inshore waters. The *Ulva* spp. spores and fronds provide an important feeding and refugia resource to the herbivorous and detritivorous invertebrates and fishes despite their common perception as a 'nuisance' species. This is an important consideration in the restoration of saltmarshes in eutrophic estuaries such as the Blackwater. The reliance on C_3 plants by herbivorous and detritivorous invertebrates and therefore older bass both in the established and restored saltmarshes, highlights the importance of protecting and restoring pioneer and other saltmarsh vegetation. In addition to their feeding value these C_3 plants in shallow zones may be the only source of refuge for invertebrates and juvenile fishes in areas where there are only dense clumps of vegetation or where there are mainly mudflats and no submerged aquatic vegetation. The breadth of basal resources ultimately adds stability to the food web on which fishes of both biological and commercial value rely.

Chapter 6: Summary, conclusions and recommendations for the design of managed realignment sites and monitoring of saltmarsh habitats for fish

Summary of main results

Throughout the year the ancient saltmarshes and newly created saltmarshes in the managed realignment sites in the Blackwater Estuary, SE England provide a habitat for fishes, the abundances of which vary with season (Chapter 3). The absence of large (3- to 5- group) predatory fishes in the catches confirms that small 0- and 1-group fish gain refuge from predation in these shallow intertidal habitats. Here juvenile bass *Dicentrarchus labrax* feed successfully on a range of prey types and in many cases they leave these habitats with fuller stomachs than when they enter them. Bass showed an ontogenetic shift in their diets, relying predominantly on zooplankton when less than 30 mm in length, while larger fish consumed progressively more benthic macroinvertebrates and terrestrial invertebrates (Chapter 4).

Managed realignment sites can provide as much food to juvenile bass as natural saltmarshes in summer, if they contain creeks, soft sediments and low access points (Chapter 4). However, by autumn, even sites with high access points and minimal soft sediment, provide bass with as much food as natural saltmarshes (Chapter 4).

At least three primary producers (C_3 plants, *Ulva* spp., and microphytobenthos) and their detritus are important basal resources of the food webs of which juvenile and small adult fishes are a part (Chapter 5). Provision of these resources is an important consideration for the conservation of existing saltmarshes and the successful creation of new saltmarsh habitats for fish.

The research has also led to the development of an inexpensive and lightweight static funnel net which can be deployed on foot in creeks and ditches or trawled through semi-permanent ponds, together with a collapsible static funnel net method which can be used to determine quantitatively the numbers of fishes using a known area of macrotidal saltmarsh within intermediate high tides (Chapter 2).

Fish assemblage

Four functional guilds of fishes (Elliott and Dewailly 1995) use the saltmarsh habitats: marine stragglers / adventitious species, marine estuarine dependents, estuarine residents and diadromous species (Chapter 4). A clear seasonal trend in the relative abundances within the fish assemblage was observed, with three main groups of fishes identified. These were from October-January when *Liza ramada* and *Liza aurata* dominated; from February-April when *Sprattus sprattus* and *Pomatoschistus microps* were dominant and from May-September when *Atherina presbyter* and *Dicentrarchus labrax* were the most abundant species. The mean density of fishes using the saltmarshes in summer was 558 0.1 ha^{-1} and the large abundance range (76 - 2699 0.1 ha^{-1}) illustrates the variability of the fish catches. The fish assemblage of the saltmarsh was different to that of the subtidal samples collected adjacent to the realignments by the Environment Agency and CEFAS. For example *Liza aurata*, *Liza ramada*, *Entelurus aequoreus* and *Sparus aurata* were caught only in the saltmarshes and not subtidally. This finding highlights the importance of integrated sampling at the landscape scale, where feasible (Hoss and Thayer 1993; Irlandi and Crawford 1997). *L.*

aurata and *S. aurata* were recorded for the first time during this study in the saltmarshes.

Bass use of managed realignment sites and saltmarshes

Juvenile bass use the established and restored saltmarshes between May and January with a peak in growth rates between July and August (1.85 % d^{-1}) and a peak in abundance between August and October (Chapter 3). The mean density of bass using the saltmarshes in summer was 233 0.1 ha^{-1} with a range of 39-951 0.1 ha^{-1} (Chapter 3). The biomass also varied considerably from 14 g 0.1 ha^{-1} when only 0-group bass used the sites, to 4544 g 0.1 ha^{-1} when 1-group bass dominated the samples.

In summer small (<30 mm) zooplanktivorous 0-group bass gained substantial feeding benefits with significantly greater gut fullness in all three managed realignment sites and established saltmarshes in the short spring tide immersion periods. Calanoid copepods were the most dominant prey item for small 0-group bass at all sites. The diets of larger *D. labrax* >30 mm were dominated by benthic macroinvertebrates, particularly *Carcinus maenas*, *Nereis* spp., amphipods, and calanoid copepods, and were more site-specific. This result is in agreement with that of Grenouillet and Pont (2001) who suggested that small juvenile fishes are less affected by habitat variables than larger juveniles. Bass that entered the low-lying, predominantly mudflat habitat of the Tollesbury managed realignment site and the low creeks within the established saltmarshes left these sites with fuller stomachs than those that colonised the higher predominantly vegetated managed realignment sites at Abbotts Hall and Orplands. However, these differences were mitigated by the opportunistic nature of bass feeding, so that by autumn when a wider range of benthic and terrestrial prey were eaten, the fishes left the three managed realignment sites with similar amounts of marsh resident food in their guts.

Sources of primary productivity

Microphytobenthos, C_3 plants and *Ulva* spp. (spores and fronds), both living and as detritus, are basal resources for herbivorous and detritivorous invertebrates which are consumed by 0- and 1-group *Dicentrarchus labrax*, 0-group *Sprattus sprattus* and *Liza ramada*, as well as juvenile and adult *Atherina presbyter* and *Pomatoschistus microps* (Chapter 5). The breadth of basal resources adds stability to the food web on which the fishes rely. The results from this study show that *Ulva* spp. blooms, typical in nutrient enriched estuaries like the Blackwater, should not necessarily be regarded as a limitation to fish feeding because of their detrimental effects on benthic invertebrates. *Ulva* spp. can smother other saltmarsh plant species and further research is required to determine the relative importance of physical impacts upon the refuge value of such sites (Deegan 2002).

C_3 halophytes, including the annual pioneer zone species, were shown to be a valuable resource for the food webs. Herbivorous invertebrates of terrestrial, freshwater and marine origin consume C_3 plants directly and indirectly as detritus. These invertebrates are consumed by larger juvenile fishes especially *Dicentrarchus labrax*. In addition to their feeding value during the summer when fish growth rates are high, these pioneer zone C_3 plants may be the only source of refuge for small fishes from fish and bird predators, in areas where there are only dense clumps of vegetation or where there are mainly mudflats with no submerged aquatic vegetation (Rozas and Odum 1987; 1988). Many authors have commented on the variables to consider when creating or restoring saltmarsh vegetation (Chapter 1). These include the position of restored sites in the estuary, the necessity to provide time for perennial vegetation to develop for positive sediment budgets and the importance of elevation of the initial surface in the tidal frame (Crooks et al. 2002; Pethick 2002) as this ultimately will determine the plant species that will colonise the new habitats.

Unvegetated habitats

The productivity of the microphytobenthos of the mudflats and their infauna are valuable to fishes, both directly and indirectly (Chapter 5). Therefore the increasing use of herbicides in the hinterland could impact upon the whole food web detrimentally by depleting the abundance of microphytobenthos (Mason et al. 2003). The soft sediment microhabitats should be restored in the most structurally complex way feasible, for example, through the use of marsh terracing in combination with vegetation, to increase the amounts of marsh edges which are particularly attractive to marsh nekton (Grenouillet and Pont 2001; Rozas and Minello 2001; Zedler 2001; Minello and Rozas 2002; Whaley and Minello 2002; Moseman et al. 2004). The threshold level above which no further enhancement is obtained from increasing the amount marsh edge (Kneib 2003) is still to be determined in these systems.

Creek and channel systems would provide soft sediments and a substrate for microphytobenthos growth for burrowing infauna and epifauna prey. Although extensive dendritic creek systems mimicking the natural marsh are a challenge to create, the focus of designs should be on shallow, broad shapes that provide a large surface area for growth of microphytobenthos as food for infauna and shallow habitats for fish. Many authors have commented on the importance of restoring dendritic creek systems and bifurcation points to provide fish access and a longer residence time to the shallowest, safest, most landward areas of the high marsh (Minello and Zimmerman

1992; Simenstad et al. 1998; Williams and Zedler 1999; Desmond et al. 2000; Eertman et al. 2002; Weishar et al. 2005). The results from Chapter 4 show that deeper creeks at the mouths and entrance to sites provide earlier access and therefore a longer foraging time to large benthic macroinvertebrate feeding 0-group bass during their main summer growth period.

The soft sediments within semi-permanent shallow ponds and scrapes could also provide substrates for MPB and infaunal invertebrate prey. They do not dry out and provide shallow refugia for small zooplanktivorous (e.g. 0-group *Sprattus sprattus*), detritivorous (e.g. *Nereis diversicolor*) and/or herbivorous (e.g. *Hydrobia ulvae* and *Liza ramada*) fish from larger fish predators. Salt pans (pools) exist at higher elevations, up to mean high water spring tide level. They rarely provide a suitable habitat for juvenile marine fish (personal observation) perhaps because they are infrequently inundated and are subject to a wide range of salinities (Fry 1988). Salt pans are more likely to be important for benthic meiofauna, which may become available to the zooplanktivorous fishes in resuspended form on high spring tides or to the abundant estuarine residents *Pomatoschistus microps*.

Estimating the economic value of saltmarshes for bass and further research

The restoration of saltmarsh habitats through managed realignment may result in a number of wide ranging potential benefits (Chapter 1). There is a need to quantify these benefits to improve the decision making and restoration process (Ledoux and Turner 2002; Rozas et al. 2005; Lawton 2007), to financially justify further schemes (Lee 2001; Pethick 2002; Knogge et al. 2004; Doody 2008), to develop budgets for the conservation of existing habitats (Sherman and Duda 1999) and to determine the scale of financial or direct habitat compensation for detrimental anthropogenic activities

(French McCay and Rowe 2003; Peterson and Lipcius 2003; Rozas et al. 2005). One element of this process should involve the estimation of the economic value of saltmarshes to recreationally and commercially important fishes (Peirson et al. 2001; Stevenson 2002; Tinch 2003). A preliminary estimate of the economic value of restored saltmarshes as suppliers of 36cm bass, *Dicentrarchus labrax* to the Blackwater inshore fishery is provided here, to highlight further areas of research.

Bass was the only economically important species caught in sufficient numbers to calculate an economic value from the three nursery habitats, despite the presence of a number of commercially important species including herring, golden and thin-lipped grey mullet, gilthead bream and sand smelt. Further research is required to quantify the benefits of saltmarshes to these and other fishes without an obvious economic market (Loomis et al. 2000; Ledoux et al. 2003). Bass older than five years were not considered in this estimate as they migrate out of the local area to spawn offshore in large numbers (Pickett et al. 2004) and can be commercially and recreationally fished. Using the quantitative fish catch data from Chapter 3, the calculated body weight of each bass was used to estimate the instantaneous natural mortality rate and percentage survival of 0- and 1-group bass to the following years, up to the 5^{th} year (36cm) when any surviving fish would then be available to the inshore fishery. The abundance and predicted body weights of the survivors were then used to estimate the market value of the bass. As is common in calculations of this sort a number of assumptions are necessary, but often these are not supported by data. The calculations were based on the following assumptions (and therefore areas for further research):

- The yield followed a steady-state stock structure and the supply of 0-group bass to the saltmarshes over time was constant

- The estuarine carrying capacity and resilience (Elliott et al. 2007), incidence of cannibalism and environmental parameters such as temperature (Henderson and Corps 1997) were constant
- There was no fishing mortality as the minimum legal landing size of bass in the Blackwater Estuary is currently 36cm
- For the 3 to 5-group cohorts the estimates were reduced by 30% to account for local losses from migration. This was based on a study by Pickett et al., (2004) who observed 70% recapture rate within tagged bass in SE England
- The current average wholesale price of a premium 'small' wild bass is assumed to be constant, ranging from £4.50 to £9.00 kg^{-1} (Fishing News: Newlyn market prices, January-September 2007 and Ian Campbell, personal communication). The market value of bass was assumed to be £4.50 kg^{-1} (minimum price) and £7 kg^{-1} (average price).
- The weight range of 36-40 cm fish was estimated to be 488.40 - 666.80 g (mean 573.01 g) (Dorel 1986 in FISHBASE 2007)
- The sites were assumed to be of a constant quality of fish habitat per hectare (Bell 1997)

Data analysis

The mean body weight (g) of each 0-group or 1-group bass collected (see Chapter 3) was estimated using the total length (cm) regression parameters calculated for a subsample of 100 gutted 0-group bass according to the formula:

$$BW\ (g) = q\ TL^{b} \qquad \textbf{(5.1)}$$

where $q = 0.0064$

$b = 3.1931$

In the absence of wild juvenile bass natural mortality data, the mean instantaneous natural mortality was calculated for each subsequent year of growth up to the fifth year, as a function of mean cohort weight (g) according to the formula after Lorenzen (1996) who used a range of natural mortalities of wild populations of predominantly temperate, juvenile and adult marine fishes to calculate M_u and b:

$$M_w = M_u W^{b} \qquad \textbf{(5.2)}$$

where M_w = natural mortality rate at weight, W

M_u = natural mortality rate at unit weight (3.69)

b = allometric scaling factor (-0.305)

The mean cohort weight was then estimated by plotting mean cohort length against weight using growth parameters estimated from bass caught in the Bay of Biscay (after Dorel 1986 in FISHBASE 2007). The instantaneous mortality rate at weight per cohort was then converted to percentage survival at weight per cohort according to the formula:

$$S = e^{-M_w} \qquad \textbf{(5.3)}$$

The primary catch data were then used to calculate the number of survivors at weight per year, up to a maximum of 5 years. The mean number of expected surviving individuals was calculated separately for 0-group and 1-group bass to estimate the total number of survivors from both cohorts. The estimates were then extrapolated for the each managed realignment sites area.

Table 6.1: The estimated value in £ (Stirling) and kilograms, of 0 and 1-group bass caught in Blackwater estuary saltmarshes in summer in units of surviving wild 5 year old, 36 cm, 573.01 g bass to the fifth year of life. The price range is for 'small' bass sold at between £4.50 (lower limit) and £7.00 (average annual price, 2007)

	Mean	Tollesbury	Abbotts Hall	Orplands
Size (hectares)	1	21	84	38
Mean Price (£)	11.82 -	159.58 -	368.31 –	288.76 -
@ £4.50/kg - £7/kg	7.60	248.23	992.93	449.18
Total weight (kg)	1.69	35.46	141.85	64.17
Mean number of 5-gp survivors	2.95	61.89	247.55	111.99

Successful saltmarsh restoration may also result in biogeochemical and socio-economic benefits. As part of the project entitled 'Combined functions in coastal zone management, ComCoast', the results presented here including the estimate of the economic value of the Blackwater Estuary managed realignment sites for bass, were combined with two other ComCoast sponsored projects on the socio-economic and biogeochemical cycling of managed realignment sites, to produce an integrated ecosystem based cost-benefit analysis of managed realignment sites in the UK.

Conclusions

The findings from this thesis show that the restored saltmarshes in the Blackwater estuary are important feeding habitats for 0-group bass *Dicentrarchus labrax*, sand smelt *Atherina presbyter*, sprat *Sprattus sprattus*, thin-lipped mullet *Liza ramada*, golden mullet *Liza aurata*; and common goby *Pomatoschistus microps*, which also feed in the saltmarshes as adults.

Microphytobenthos, fresh and detrital C_3 plants and *Ulva* spp., are all important sources of productivity for small fishes that consume zooplankton and benthic meiofauna (15-29 mm) and larger bass (30-59mm) which consume macroinvertebrates. These sources of productivity and the trophic interactions that relate to them, can be maintained by developing managed realignment sites with creeks, soft sediment and vegetated microhabitats, thereby improving the stability of the saltmarsh food web. The restoration of saltmarsh fish feeding grounds should be an important consideration in the management of estuarine-dependent marine fish stocks.

There is a general need to improve our global understanding of the ecology of post-larval fish in inshore habitats, in order to determine the impacts of climate change, such as increasing sea-surface temperatures and sea-level rise, on the spatio-temporal variations in saltmarsh fish communities. The work reported here is a contribution towards this goal.

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